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The taxonomy and distribution of the phylum Tardigrada in Montana west of the Continental Divide

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THE TAXONOMY AND DISTRIBUTION OF THE PHYLUM TARDIGRADA IN MONTANA WEST OF THE CONTINENTAL DIVIDE

by

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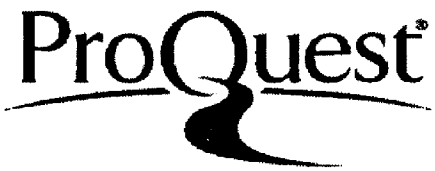

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The Distribution and Taxonomy of the Phylum Tardigrada in Montana West of the Continental Divide (132 pp.)

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Representitives of five genera (twenty species) of the phylum Tardigrada were studied to determine the distribution and taxonomy of members of the phylum which occur west of the Continental Divide in the State of Montana, U. S. A.

The collection of specimens established initial records of the occurence of members of the phylum in Montana and established initial and corroborative records of the species of Tardigrada which were studied for North America. Hysibius (Diphascon) arduifrons was collected from the North American Continent for the first time. The collection of Hypsibius (D.) spitzbergensis, Echiniscus quadrispinous, and Echiniscus tristerosus constituted the second report of these species from North America. Macrobiotus areolatus, Macrobiotus islandicus, Hypsibius (D.) alpinus, Hypsibius (I.) prosostomus, Echiniscus arctomes, Pseudechiniscus raneyi, and Pseudechiniscus victor were reported from North America for the third time. Members of nine more ubiquitous species, including Macrobiotus harmsworthi, Macrobiotus hufelandii, Macrobiotus richtersi, Hypsibius (D.) angustatus, Hypsibius (D.) oculatus, Hypsibius (D.) scoticus, Hypsibius (H.) convergensis, Hypsibius (H.) oberheauseri, and Milnesium tardigradum, were also collected.

The habitats which were utilized by the specimens were reported. General conditions of the environment were also noted.

Two mathamatical measures of association, Chi-square and Cole's Coefficient, were applied to the data. The results were inconclusive.

A key to the species of the Tardigrada which were found in western Montana was constructed.

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Most of all, I should like to express my sincere thanks to my wife, Linda, without whose encouragement, editing and secretarial skills this work might not have been completed.

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CHAPTER I

INTRODUCTION

This study was undertaken for three reasons: (1) to survey the species of the phylum Tardigrada in Montana west of the Continental Divide; (2) to collect ecological data on these species; and (3) to construct a key for the identification of these species.

The interest in this problem stemmed from the lack of records of the occurrence of these animals in Montana.

Tardigrades were first discovered and described almost two hundred years ago by Goeze (1773), who called them "Kleiner Wasserbaer." Since that time, there have been approximately three hundred papers and notes in which tardigrades have been mentioned. This is a relatively small number of scholarly works concerning animals so common in nature and so easily collected in large numbers.

According to Mathews (1938), "Illiger, Cuvier, Burmeister, and others originally applied the name Tardigrades to a group of mammals." Spallanzani (1776) used the name "Il tardigrade" for these animals. Dalyell (1830) used the term "sloth" to describe tardigrades. Huxley (1869) coined the present terms of "waterbear" and "watersloth" which described the characteristic slow movements of tardigrades.

Packard (1873) found the first tardigrades from North America in samples from Gloucester, Maine. Beal (1880) also recorded a tardigrade from the same area.

Murray (1907) published a list of tardigrades and included a Hysibius from North America without stating where it was collected. Richters (1908) wrote of tardigrades from British Columbia. Murray (1910) published a list of tardigrades from the findings of E. Shackleton's expedition, 1907-1909, which included tardigrades from North America.

North America's first marine form of tardigrade, Batillipes mirus, was described by Hay (1917) from Beaufort, North Carolina. Marcus (1928) mentioned the finding of a member of the Macrobiotidae at Washington, D. C., and at Niagara Falls.

Marcus (1929) wrote the first monograph on this group.

Mathews (1938) reviewed all previous work in his "Tardigrada from North America," which included a list of twelve species and all known collections in America north of Mexico to that date.

The papers and notes that have appeared since Mathews' work have increased the number of tardigrade species found in the United States from the twelve species reported by Mathews to almost fifty reported by Schuster and Grigarick (1965).

Curtin (1948) collected tardigrades in the District of Columbia. Chitwood (1951, 1954) reported on both a marine form and the non-marine forms of the Gulf Coast. Crisp and Hobart (1954) noted the habitat of Echinscoides sigismundi. Le Gros (1955) added some general information. The tardigrades of Maryland were studied and subsequently reported by Curtin (1957).

Pigon and Weglarska (1955) studied the metabolic rates in both cryptobiotic and active phases of tardigrade life. Keilin (1959)

considered the problems of cryptobiosis and latent life.

Puglia (1959) worked with the Tardigrada in central Illinois. Higgins (1959) studied and reported on the life history of Macrobiotus islandicus and other tardigrades from Colorado. Baumann (1960) reported on collections in Colorado and Utah. Higgins (1960) reported on the tardigrades of North Carolina. Boudrey (1960) published on the forms of Minnesota. Riggin (1962, 1964) contributed to the knowledge of the animals in Virginia, North Carolina and South Carolina.

Riggin (1962) also reviewed for the first time in English the arguments for considering the Tardigrada as a phylum. The latest monograph by Ramazzotti (1962) provides the most recent and complete systematic treatment of the phylum.

Schuster and Grigarick (1965) studied and reported upon the tardigrades of the Pacific Coast, especially those in California.

CHAPTER II

DESCRIPTION OF STUDY AREA

Western Montana, as treated in this paper, consists of that area in Montana west of the Continental Divide. This area, of approximately 25,000 square miles, is drained by the Kootenai River and by the Clark Fork of the Columbia River. The Kootenai River drains a large portion of British Columbia before entering Montana. The Clark Fork of the Columbia can be divided into seven major watersheds (map #1). They all originate in western Montana, with the exception of the North Fork of the Flathead River, which enters from British Columbia.

Western Montana is characterized by a series of mountain ranges and intervening valleys (map #2). North of Missoula, these mountain ranges extend northwest and parallel the Continental Divide. South of Missoula, these ranges are orientated north to south. The major exception is the Anaconda Range on the southern edge of the area, which lies east to west.

Elevations range from above ten thousand feet (3,400M) in the mountains to twenty-five hundred feet (840M) in the lower valleys. The vegetation ranges from alpine on the high peaks, through thick coniferous forests, to the bunch grass prairies of the river valleys.

CHAPTER III

MATERIALS AND METHODS

There are no standard techniques for collecting tardigrades. The "hand full" seems to be the only quantitative measure used in sampling.

Selection of possible tardigrade-bearing habitats depended upon on the variety of suitable habitats which were present; they ranged from higher plants through mosses and lichens to fungi. Plants thought to be suitable habitat for tardigrades were collected by hand. The sites were selected from a map to provide coverage of the study area.

For each collection, a sample of material was taken to half fill a quart plastic bag. The bag was numbered for the site and lettered for the sample distribution within the site. Data recorded at the time of collection included: collection code, date, location, habitat of sample, and type of sample. Plant identifications, slide numbers and animal identifications were added to the records as the samples were processed. The exact location by range, township, and section was obtained from United States Forest Service maps.

Each sample was brought into the laboratory, where it was divided. One-half was dried for the plant collection and the other half was trimmed to fit into a finger bowl to which 150 ml. of water was added. The bowls were allowed to stand undisturbed for 48 hours, at which time enough water and debris from the bottom of the bowl was drawn off to half fill a petri dish.

The contents of the dish were inspected with a dissecting microscope under 45 power with transmitted light. The asphyxiated tardigrades were transferred with a micropipette to vials of 70 percent alcohol tinted with iodine stain.

The specimens were stored in these vials until the animals were mounted on microscope slides in Hoyer's medium. Slide preparation was facilitated by a 15 power dissecting microscope and a micropipette.

The animals were placed on the slide, and Hoyer's medium was added. With the aid of an insect pin, the animals were centered. When the cover slip was in place without support, the position of each animal was observed, marked, recorded and coded for later identification.

Identification was made with a compound microscope.

The keys of Schuster and Grigarick (1965), Pennak (1953), and Marcus (1959) were used for initial identification. In some cases, consultation with Robert O. Schuster at the University of California at Davis was necessary for positive identification. Mr. Schuster confirmed all identifications.

Riggin's (1962) standards of small, medium and large were used. A classification of small includes lengths up to 250u, medium includes those forms from 250-500u in length, and large is used for those over 500u in length. Only fully extended animals were measured.

CHAPTER IV

THE PHYLUM TARDIGRADA

Tardigrades are aquatic invertebrates. They are found in unique aquatic habitats. Many species occur in the droplets or film of water on mosses, lichens, liverworts, and angiosperms. They have been found in the capillary water between the grains of sand on both fresh and salt water beaches. Some forms are completely fresh water and some are marine. Tardigrades have even been collected from the moist leaves of forest litter.

Tardigrades are found worldwide: arctic, antarctic, temperate, and tropic regions. Although Tardigrades are widely distributed, the temperate latitudes have a greater concentration of numbers and species than do the tropics. The animals have even been found at altitudes of eighteen thousand feet. The most likely place to find a tardigrade is in a sample of damp moss.

Tardigrades have a head and four body segments; from each body segment arise a pair of legs. Each leg ends in four claws or a pair of double claws. The mouth is anteriad, ventrad or subterminal. The cloaca is between the base of the fourth pair of legs. The body is covered with a cuticle secreted by the thin hypodermis of polygonal cells. Sexes are separate (Pennak, 1953).

Materials diffuse and circulate within the body fluid, and

respiration presumably occurs through the body surfaces, thus explaining the lack of circulatory and respiratory systems (Pennak, 1953).

Tardigrades are thought to be chiefly preyed upon by amoeboid protozoans, nematodes, and possibly by each other (Pennak, 1953).

The animals exhibit four phases of life other than the egg: (1) active, (2) cryptobiosis, (3) asphyxia, (4) cyst (Pennak, 1953).

ACTIVE: In this phase, the animal is supple and crawls around like a small caterpillar. It used the stylets to pierce stalks of moss for food. One species is known to prey on nematodes. All development, growth, reproduction, egglaying, and feeding takes place during this phase of life.

CRYPTOBIOSIS: In this phase, the integument of the animal wrinkles as the body volume is reduced, eventually ending in a cask shape with the legs and eyes barely distinguishable. Cryptobiosis is believed to be caused by the desiccation of the animal's surroundings. As the amount of moisture and the available oxygen supply associated with the moist environment diminish, the signs of life decrease until the animal is completely dry.

With the return of moisture, the animal regains its shape and suppleness and returns to the active phase. Mathews (1938) states that one animal had been observed to exhibit the state of cryptobiosis fourteen times.

ASPHYXIA: In this phase, the antithesis of cryptobiosis, the cells of the hypodermis lose the ability to control the movement of water across their membranes and, consequently, absorb too much water.

This distends the cells and stretches the whole animal. The animal is unable to move in this phase but will survive for about five days before dying. The animal is at the complete mercy of its environment. Marine and aquatic forms do not exhibit this phase.

ENCYSTING: In this phase, damage, hunger, and other abnormal ecological conditions sometimes bring about the formation of resistant cysts, especially in the aquatic forms. The animal contracts inside its old, wrinkled cuticle and forms a dark colored, thick-walled cyst. The internal organs undergo variable degrees of degeneration. When ecological conditions become favorable, the animal is reconstituted. The cyst wall ruptures, and the tardigrade emerges.

A simplex stage, which is thought to be a tardigrade about to encyst or just emerging from a cyst, displays a reduced buccal apparatus. The macroplacoids are abortive, the esophagus is reduced and slender, and the stylets are reduced to nonfunctional state. Sometimes all of the digestive system anteriad of the stomach disappears and there is no mouth (Pennak, 1953).

Although asphyxia is valuable to the animal in preventing drowning during periods of excess water, the cryptobiotic phase is by far the most useful to the animal in survival and distribution. Some authors have suggested that the cryptobiotic phase may be transported by wind.

Franceschi (1948) demonstrated in the laboratory that a tardigrade which had been in the cryptobiotic state for one hundred twenty years was returned to the active phase with the addition of moisture. Rahm (1924, 1926) subjected cryptobiotic tardigrades to minus 200 degrees centigrade for twenty-one months without impairing their ability to

survive. Likewise, Bacquerel (1950) took cryptobiotic animals to 0.05 degrees centigrade for fifteen minutes (Rahm, 1924, 1926), one thousand atmospheres of pressure, vacuums and high concentrations of gases such as hydrogen sulfide and carbon dioxide (Baumann, 1922). The cryptobiotic state of tardigrades demonstrated resistance to ultraviolet light (Rahm, 1922), and X-rays (May, et al, 1964).

It appears that this range of resistances allows little doubt concerning tha animal's ability to survive; however, it raises many questions as to how an animal of this nature has evolved these capabilities.

Taxonomy

Marcus' (1928) classification of the Tardigrada was followed for many years. He listed the Tardigrada as PROSTOMIA ARTICULATA (Annelida and Arthropoda), placing them between the PROTRACHEATA and the EUTRACHEATA. He further subdivided the group as:

Order HETEROTARDIGRADA
- Suborder Arthrotardigrada, two families
- Suborder Echiniscoidea, two families

Order EUTARDIGRADA, two families

Ramazzotti (1962) revised Marcus' classification. He established three Orders, EUTARDIGRADA, MESOTARDIGRADA, and HETEROTARDIGRADA.

Order MESOTARDIGRADA
- Family Thermozodidae
  - Genus *Thermozodium*

Order EUTARDIGRADA
- Family Macrobiotidae
  - Genus *Macrobiotus*
  - Genus *Haplomacrobiotus*
  - Genus *Hypsibius*

Genus Itaquascon
Family Milnesiidae
Genus Milesium

Order HETEROTARDIGRADA
Suborder ARTHROTARDIGRADA
Family Stygarctidae
Genus Stygarctus
Family Batillipedidae
Genus Batillipes
Genus Orzeliscus
Family Halechiniscidae
Genus Halechiniscus
Genus Actinarctus
Genus Tetrakentron
Genus Styraconyx
Genus Tanarctys
Genus Bathyechiniscus

Order HETEROTARDIGRADA
Suborder ECHINSCOIDEA
Family Oreellidae
Genus Oreella
Genus Echiniscoides
Genus Archechiniscus
Family Echiniscidae
Genus Echiniscus
Genus Parenchiniscus
Genus Pseudechiniscus
Genus Mopsechiniscus

The classification by Ramazzotti (1962) has been followed since its introduction. It is the system followed in this paper.

The identification of a tardigrade is based upon its size, cuticle, claws, and mouthparts. Eggs are also useful in identification for some species.

The classification by size includes: small up to 250u, medium from 250-500u, and large over 500u.

The cuticle may be smooth, granular, tuberculate, or spiney, as in the Eutardigrada. The animals may be covered with cuticular plates which may or may not have spines, as in the Heterotardigrada.

The legs terminate in one or many claws, except in the family Batillepedidae, which has four digits on each foot. Each digit is expanded distally to form adhesive discs.

Claws may be of many sizes and shapes, and each is a general guideline to the identification of a group of tardigrades. Macrobiotidae exhibit claws each with similar branches from a common base. Milnesiidae have the principal and secondary branches of the claws separated. Tardigrades of the suborder Echiniscoidea have separate claws, four on each foot, and are further differentiated by the presence or absence of a spur. Members of Halechiniscidae have legs ending in separate digits, each terminating in a claw.

Eyespots do not seem to be definitive characteristics, although in some groups their presence or absence is helpful in identification.

The mouthparts of tardigrades are divided into three main sections: buccal tube, pharyngeal tube, and pharynx. The characteristics of each section can be diagnostic in determination of species.

The buccal tube is the most anteriad of the sections, and is composed of the mouth, stylets, stylet supports, and the tube itself.

In Heterotardigrada, the stylets are parallel or adjacent to the buccal tube, but no stylet supports exist. In Mesotardigrada and Eutardigrada, the buccal tube extends only as far as the stylet supports. It is slightly thickened and has, at its anterior end, a buccal ring and a stylet sheath. The stylet and stylet supports join to form the furca. The buccal tube may have a support apparatus called an apodeme.

The pharyngeal tube of Mesotardigrada and Eutardigrada is that part of the tube between the stylet supports and the pharynx. It varies

in length and width depending on the species. The pharyngeal tube ends with an enlargement within the pharynx called an apophysis. In Heterotardigrada, there is no pharyngeal tube, the buccal tube opens directly into the muscular pharynx.

The pharynx may be characterized by the presence of sclerotized placoids. The thin placoids of the Heterotardigrada seem to be attached directly to the buccal tube. Within the pharynx of Mesotardigrada and Eutardigrada, there may be two or three sets of macroplacoids numbered from the anterior to the posterior. The last placoid may be small in comparison to the previous placoids and is termed a microplacoid. An additional sclerotized structure posteriad to the microplacoid is called a septulum. Pharyngeal shape and placoid size, shape, and arrangement are considered good taxonomic characters.

List of Tardigrada from Western Montana

Phylum TARDIGRADA

Order Eutardigrada
Family Macrobiotidae
Macrobiotus Schultze, 1834

Macrobiotus areolatus Murray, 1907
Macrobiotus harmsworthi Murray, 1907
Macrobiotus hufelandi Schultze, 1834
Macrobiotus islandicus Richters, 1903
Macrobiotus richtersi Murray, 1911

Hypsibius Ehrenberg, 1848

Subgenus *Diphascon* Plate, 1889

Hypsibius (*Diphascon*) *alpinus* (Murray, 1906)
Hypsibius (*Diphascon*) *angustatus* (Murray, 1905)
Hypsibius (*Diphascon*) *arduifrons* (Thulin, 1928)
Hypsibius (*Diphascon*) *oculatus* (Murray, 1906)
Hypsibius (*Diphascon*) *scoticus* (Murray, 1905)
Hypsibius (*Diphascon*) *spitzbergensis* (Richters, 1903)

Subgenus Hypsibius Thulin, 1928

Hypsibius (Hypsibius) convergens (Ubanowicz, 1925)
Hypsibius (Hypsibius) oberhaeuseri (Doyere, 1840)

Subgenus Isohypsibius (Thulin, 1928)

Hypsibius (Isohypsibius) prosostomus (Thulin, 1928)

Family Milnesiidae

Milnesium Doyere, 1840

Milnesium tardigradum Doyere, 1840

Order Heterotardigrada

Suborder Echiniscoidea

Family Echiniscidae

Echiniscus Schultze, 1840

Echiniscus (Echiniscus) arctomys Ehrenberg, 1853
Echiniscus (Echiniscus) quadrispinosus Richtersi, 1902
Echiniscus (Echiniscus) trisetosus Cuenot, 1932

Pseudechinscus Thulin, 1911

Pseudechiniscus raneyi Grigarick, Mihelcic, & Schuster, 1964
Pseudechiniscus victor Ehrenberg, 1853

Key to the Species of Tardigrada from Western Montana

1. Lateral cirrus A present at posterior margin of plate A. 16
1. Lateral cirrus A absent, dorsal plates absent 2

2. Six rostral papillae surrounding mouth opening Milnesium tardigradum
2. Mouth not surrounded by papillae 3

3. Claws of each foot equal in size and shape Macrobiotus 4
3. Claws of each foot not equal in size and shape Hypsibius 8

4. Three separate macroplacoids present 5
4. Two macroplacoids present, or if questionably three, first two contiguous 7

5. Microplacoid present 6
5. Microplacoid absent *Macrobiotus areolatus*

6. Length of pharyngeal tube subequal to width of buccal tube, macroplacoids elongate *Macrobiotus richtersi*
6. Pharyngeal tube longer than width of buccal tube, macroplacoids globular, not long *Macrobiotus harmsworthi*

7. First macroplacoid much longer than second; microplacoid present *Macrobiotus hufelandii*
7. First macroplacoid slightly longer than second, microplacoid absent *Macrobiotus islandicus*

8. Pharyngeal tube flexible, longer than one-half length of pharynx 9
8. Pharyngeal tube not flexible, less than one-half of pharynx 14

9. Three macroplacoids 10
9. Two macroplacoids, with or without microplacoid 12

10. With microplacoid 11
10. Without microplacoid *Hypsibius* (*D.*) *arduifrons*

11. Pharyngeal tube more than twice length of placoids; placoids granular *Hypsibius* (*D.*) *alpinus*
11. Pharyngeal tube less than twice length of placoids; placoids narrow rods *Hypsibius* (*D.*) *scoticus*

12. First macroplacoid longer than second *Hypsibius* (*D.*) *oculatus*
12. First macroplacoid shorter than second 13

13. Pharyngeal tube thick, distinctly annulate, approximately as long as macroplacoids, Microplacoid absent *Hypsibius* (*D.*) *angustatus*
13. Pharyngeal tube thin, distinctly annulate, approximately as long as macroplacoids, microplacoid present *Hypsibius* (*D.*) *spitzbergensis*

14. Secondary branch of external claw continuous arch with base
15

14. Secondary branch of external claw forming right angle with base
Hypsibius (*I.*) *prosostomus*

15. Two macroplacoids, dorsum reticulate sculpture, principal branch of external claw appreciably wider at base than near apex
Hypsibius (*H.*) *convergens*

15. Two macroplacoids, dorsum reticulate sculpture, principal branch of double claw long, thin, not appreciably wider at base than at apex
Hypsibius (*H.*) *oberhaeuseri*

16. Terminal plate E directly behind plates D, or with only intersegmental (median) plate interposed
17

16. Terminal plate E separated from plates D by transverse plate or plate pair (pseudosegmental plate)
19

17. Only lateral spine A present
Echiniscus (*E.*) *arctomys*

17. More than lateral spine A present
18

18. Lateral spine E present, collar on leg IV smooth
Echiniscus (*E.*) *quadrispinosus*

18. Lateral spine E absent, collar on leg IV serrate
Echiniscus (*E.*) *trisetosus*

19. Dorsal spines C & D present, buccal cirri bifurcate
Pseudechiniscus victor

19. Dorsal spines C & D absent, buccal cirri simple
Pseudechiniscus raneyi

CHAPTER V

SYSTEMATIC TREATMENT

Genus Macrobiotus Schultze, 1834

The genus Macrobiotus is characterized by the double claws of each leg equal in size and identical in shape to the others. The cuticle is smooth or papillose. Eyespots may or may not be present. Mouthparts are stout, conspicuous mechanisms. Placoids are generally large, and occupy most of the pharynx. The buccal tube is longer than the pharyngeal tube, and may be supported by a single longitudinal apodeme on the ventral side. The stylets and stylet supports are present, furcae are usually well developed. The macroplacoids may be present in some species.

Five species of Macrobiotus were collected during this study.

Macrobiotus areolatus Murray, 1907

Originally described by Murray (1907) as a new variety of Macrobiotus echinogenitus Richters, Macrobiotus areolatus was elevated to specific status by Murray (1910), but placed in the genus Hypsibius.

> "Distinictive Characters. - Of large size, up to 800u. Eggs very large, up to 180u over spines, or 95u without spines; spines papillose, separated at the bases, the intermediate surface of the shell marked with irregular polygonal spaces, symmetrically arranged. The claws are united for a short distance at the base. The pharynx has three narrow rods, nearly equal, and no comma. Claws of largest examples 40u long; fat cells up to 15u long.

> Spitsbergen and Franz Josefland; also known from mountain tops in Shetland, and the mainland of Scotland, the Himalaya, etc...
>
> After the characters of the egg, the most striking difference is the absence of comma in the pharynx. Many young have been seen to issue from eggs. The teeth are not acicular, but broad and lance-shaped at the ends. Each long claw has two supplementary points."

Macrobiotus areolatus from Montana.

Three specimens of Macrobiotus areolatus have been collected in western Montana. Average length 403u, excluding legs IV, range of measurements from 260u to 550u. Cuticle smooth, eyespots present. Three macroplacoids present in anterior three/fourths of pharynx, no microplacoid. First two macroplacoids nearly equal in length, third shorter. Buccal tube wide, pharyngeal tube short. Stylet supports at anterior edge of pharynx.

Macrobiotus areolatus from North America.

Described by Murray (1907) as a new variety of Macrobiotus echinogenitus, Richters, Macrobiotus areolatus was first reported from North America in 1910 by Murray, who, according to Mathews (1938), placed the forms from British Columbia in the genus Hypsibius. Marcus (1929) followed this classification but expressed doubts in 1945 according to Ramazzotti (1962) as to the validity of the genus Hypsibius for this species.

Macci (1951-52) examined several thousand individuals and concluded on the basis of claw structure that the genus should be Macrobiotus.

This scheme is followed by Petersen (1951), Ramazzotti (1958), and Ramazzotti (1962).

Since Murray's work in 1910, only Schuster and Grigarick (1965) have reported Macrobiotus areolatus from North America.

This paper constitutes the third report of Macrobiotus areolatus from North America.

Macrobiotus areolatus, ecology notes.

Schuster and Grigarick (1965) reported Macrobiotus areolatus from twenty-four samples of mosses, twenty-four samples of lichens, a liverwort, a clubmoss, and seven unidentified habitats. Schuster and Grigarick (1965) do not give identification of these plants to species.

Three specimens were found in western Montana. One was removed from an intermingled mass of the mosses Claopodium blanderi and Rhytidiaelphus trigustrus, the second was found in the moss Homalothecium occidentali, and the third was removed from an unidentified plant. These three collections were all from the western slopes of the Mission Mountains in the Flathead River drainage.

Among the other species of tardigrades removed from these samples, it was noted that Macrobiotus hufelandii was found in all three samples; and that one sample also yielded Hysibius (D.) spitzbergensis, a species of which only four individuals have been reported from North America.

All known collections of Macrobiotus areolatus in North America are from the Pacific slope. Higgins (1959) working in Colorado, Puglia

(1959) in Illinois, and Riggin (1962) in Virginia did not report this species.

Ramazzotti (1962) stated that the animal is cosmopolitan and common in Italy.

Macrobiotus harmsworthi Murray, 1907

> "Specific Characters. - Size moderate, blood pale yellow. Teeth nearly straight, with bearers; pharynx somewhat long, oval; thickenings four in each row; first, short, attached to the gullet, second, third and fourth narrow rods, the fourth a little longer than the others. Claws of hufelandi-type, united half way, one claw of each pair much longer, with two large supplementary points. A crescent-shaped ridge in front of each pair of claws, crenate on the last legs, plain on the others. Eyes very small.
>
> Length up to 500u, pharynx 52u, claws 24u.
>
> Cape Mary Harmsworth, Franz Josef Land, Spitzbergen. Also in Shetland."

Macrobiotus harmsworthi from Montana.

One hundred nine specimens of Macrobiotus harmsworthi, have been collected from western Montana. Average length 352u, excluding legs IV, range of measurements 261u to 505u. Cuticle smooth, eyespots present. Claws similar to M. hufelandii. Wide buccal tube, stylet supports four-fifths of distance from mouth to pharynx. Pharynx large, muscular with three macroplacoids and a microplacoid. Third macroplacoid normally largest, second normally smallest.

Macrobiotus harmsworthi from North America

Macrobiotus harmsworthi was first reported from North America at Ottawa, Canada, by Murray (1910). Ramazzotti (1956) collected the first examples of this species from the United States, at Mount

Palomar, California. Higgins (1959) reported this species from Colorado, and Puglia (1959) found examples in Illinois.

Riggin (1962) reported fifty-three specimens from North and South Carolina, Virginia and Tennessee. Schuster and Grigarick (1965) uncovered more than three hundred specimens in Arizona, California, Oregon and Washington.

One hundred nine individuals of Macrobiotus harmsworthi were collected in western Montana from twenty-nine samples.

Macrobiotus harmsworthi, ecology notes.

Higgins (1959) collected twenty-six specimens from five grams (dry weight) of the moss Grimmia calyptrata. The one sample of Grimmia calyptrata found in Montana during this study was found on the East Fork of the Bitterroot and was completely without tardigrades.

Puglia (1959) found Macrobiotus harmsworthi in three of his "forest litter" samples but does not report it from any of his moss or lichen samples. Riggin (1962) gave excellent location information but said nothing of the habitat.

Schuster and Grigarick (1965) did not report the plants by species but did classify them by type and attempted to define the substrate on which those plants were found. More than half of the samples that yielded Macrobiotus harmsworthi were lichens or lichen-moss combinations.

Trees appeared to be the favored substrate for the plants that contained Macrobiotus harmsworthi.

The work in Montana showed soil and rock as the favored substrate of both mosses and lichens that yielded Macrobiotus harmsworthi.

Only six plant samples were lichens, twenty-two were mosses and one was a vascular plant. Of the six lichens, three came from trees, two from soil and one from a rock substrate. Only one of the mosses, Polytrichum juniperinum, was found in a tree.

Macrobiotus harmsworthi is a cosmopolitan species with known distribution in: Greenland, Iceland, Spitzbergen, Faroe Islands, Germany, Spain, Italy, Scandinavia, Asia, Sumatra, Australia, Canada, Mexico, Brazil, Columbia, Chile, and the United States (Riggin 1962).

Macrobiotus hufelandii Schultze, 1834

> "M. Hufelandii: Copore minimo 1/24"'- 1/3"' longo, flavo cincero, pedibus quadrangulatis."

Macrobiotus hufelandii from Montana.

Four hundred fifty-nine specimens of Macrobiotus hufelandii have been collected in western Montana. Average length 462u, excluding legs IV, range of measurements from 253u to 590u, cuticle smooth, eyespots often present. Claws stout, equal in size. Buccal tube narrow with well developed stylets; large muscular, slightly oblong pharynx. Two macroplacoids and one microplacoid. First macroplacoid constricted at middle and may appear to be separated, giving the appearance of three equal macroplacoids.

Macrobiotus hufelandii in North America.

Richters (1908) found Macrobiotus hufelandii on Vancouver Island, British Columbia. Murray (1910) also reported this species from

Canada. Marcus (1928) reported the first collection in the United States at Washington, D. C. Mathews (1938) stated, "a good population was found from San Juan Island, Washington, also Ephraim, Wisconsin, and on Isle Royal, Michigan." East Troy, Wisconsin, also yielded Macrobiotus hufelandii to Mathews. Curtin (1948, 1957) reported this species in Washington, D. C., and Maryland.

Higgins (1959) indicates the presence of two possible subspecies of Macrobiotus hufelandii in his paper on the Tardigrada of Colorado; Baumann (1960) also collected Macrobiotus hufelandii in Colorado. Puglia (1959) collected this species extensively in central Illinois; Higgins (1950) reported it from North Carolina. Riggin (1962) found Macrobiotus hufelandii abundant in North Carolina, Virginia, Tennessee, and Kentucky.

Schuster and Grigarick (1965) also found this species common in their collections from Alaska, Arizona, California, Idaho, Oregon, and Washington.

Four hundred fifty-nine specimens were collected in western Montana.

Macrobiotus hufelandii, ecology notes.

Puglia (1959) reported one hundred eighteen samples with Macrobiotus hufelandii. Of these samples, seventy-nine were lichens, thirty-four were mosses, three were forest litter, and two were grasses. Puglia did not report any of the species of plants which were collected, nor did he report substrate for those plants.

Higgins (1959) collected ninety-three Macrobiotus hufelandii from a sample of moss, Dicranum sp. The Montana collection contains twelve examples of mosses of the genus Dicranum; of these twelve, two were without tardigrades and only four contained Macrobiotus hufelandii.

Riggin (1962) found Macrobiotus hufelandii in one hundred ninety-four out of four hundred four moss samples, or forty-eight percent of his collection. He neither mentions lichens or other habitats, nor does he report any identification of his mosses. Riggin does state:

> "Two specimens of M. hufelandii were observed feeding on nematode larvae and following the mounting procedures, it was apparent that the individuals had attached themselves to the larvae by the use of the lamellae of the mouth rings. The mechanics of clearing and mounting had not altered this attachment. This is the first report of M. hufelandii feeding in such a manner."

Schuster and Grigarick (1965) found Macrobiotus hufelandii in one hundred two out of three hundred thirty-eight samples collected in the west coast states. Plant type and substrate were reported wherever possible. This species was recorded from forty lichens, thirty-eight mosses, seventeen moss and lichen combinations, and other habitats. In thirty-six samples, trees were the favored substrate of the plants bearing Macrobiotus hufelandii; soil was the substrate in nineteen samples; and rocks were noted as substrate in fifteen samples. In the remainder, the substrate was not mentioned.

In western Montana, Macrobiotus hufelandii were collected from thirty-five samples of moss, five samples of lichens, one sample of vascular plant, and one sample of a fungus.

Known to be cosmopolitan, Macrobiotus hufelandii has been reported from Greenland, Iceland, Scandinavia, Germany, France, Spain, Portugal, Ireland, Scotland, Italy, Asia, Canada, United States, Brazil, Columbia, Yugoslavia, Belgian Congo, and China (Riggin, 1962).

Macrobiotus islandicus Richters, 1903

The original description is unavailable.

Macrobiotus islandicus from Montana.

Two specimens of Macrobiotus islandicus were collected from western Montana. Length 271u, and 352u, excluding legs IV. Cuticle smooth, eyespots present. Claws of the type found in Macrobiotus hufelandii. Nearly straight pharyngeal tube leads directly into a slightly oval pharynx. Pharynx contains two macroplacoids, of which the first is the larger. First macroplacoid may be indented but not separated into two placoids. No microplacoid present. Stylet supports attach to buccal tube just anteriad of pharynx.

Macrobiotus islandicus from North America.

Described by Richters in 1903, this animal was not found in North America until 1959, when Higgins reported on its life history in Colorado. Schuster and Grigarick (1965) reported having found specimens in Alaska, Arizona, California, Oregon, and Washington. The collection of the species from Montana constitutes the third report of the occurrence of Macrobiotus islandicus from North America.

Macrobiotus islandicus, ecology notes.

Higgins (1959) reported the collection of nine hundred sixty-one specimens from the moss Tortula ruralis in Colorado. The single collection of this same plant from Montana yielded no tardigrades. Two mosses did yield Macrobiotus islandicus, Pohlia nutans and Leptodicym riparium; two examples of the former and one example of the latter were collected.

Shuster and Grigarick (1965) did not identify the plants to species but did supply data on plant type and substrate. Macrobiotus islandicus was found in forty-six samples; nineteen of these were lichens, fourteen were mosses, eleven were moss-lichen combinations, one was a bog, and one was an alga. Trees were the most common substrate for the flora in which Macrobiotus islandicus was found. Out of thirty-three substrates defined, trees accounted for twenty-four, eight were rocks and soil was the substrate in one case. Both mosses in which Macrobiotus islandicus was found in Montana were on a soil substrate.

In addition to those sites reported from North America, Macrobiotus islandicus is also reported from Europe, Greenland, and Iceland (Shuster and Grigarick, 1965).

Macrobiotus richtersi Murray, 1911

> "Specific Characters. - Large, strongly pigmented; no eyes. Teeth thick; gullet very wide; three narrow rods in pharynx, and a small "comma" distant from the last rod. Claws of hufelandi-type, joined for half the length of the longer one, which has two supplementary points. Processes of egg conical, truncate, and slightly expanded at apex; egg-surface between the processes areolate.
>
> Length 750 to 1,000u. Gullet about 16u in width. Pharynx shortly oval, 80u in length; first and second rods about four times as long as broad, third five times as long. The pattern on the egg surface is symmetrical, and consists of obscure polygons, which appear to have originated as

> regular hexagons, each divided by a partition into two equal pentagons. The processes are faintly papillose; the expansion of the apex varies in amount, and it is bordered by a circlet of papillae. The egg measures 120u over the processes, 75u without them."

Macrobiotus richtersi from Montana.

Ninety specimens of Macrobiotus richtersi were collected from western Montana. Average length 513u, excluding legs IV, range of measurements 370u to 620u. Cuticle smooth, eyes generally absent. Color: colorless, white, or brown. Buccal tube wide, pharyngeal tube short and wide. Pharynx stout with three macroplacoids. First two macroplacoids may be adjacent. All macroplacoids irregularly shaped, third may have bulb on posterior end. Microplacoid present. Stylet supports stout and short. Claws of the type found in Macrobiotus hufelandii.

Macrobiotus richtersi from North America.

Puglia (1959) was the first to report this species from North America and the United States. It occurred widely in his collections from Illinois. Higgins (1960) reported this species from North Carolina. Riggin (1962) increased the known sites of collection with specimens from Virginia and Tennessee.

Schuster and Grigarick (1965) have found the animal in California, Idaho, and Oregon.

Ninety specimens of Macrobiotus richtersi were recovered from western Montana during this study.

Macrobiotus richtersi, ecology notes.

Puglis (1959) collected Macrobiotus richtersi from ten samples of forest litter and two samples of moss. He reported the animals as large, ranging from 750u to 1,000u, and as having a color which varies from colorless to brown.

Higgins (1960) mentioned having seen two specimens of Macrobiotus richtersi feeding on rotifers. This is the only mention of carnivorous habits by this animal.

Riggin (1962) recovered sixteen specimens which ranged in size from 232u to 759u, but made no comment on the color of the animals, nor did he include any information relating to the habitats of the animals.

Schuster and Grigarick (1965) found Macrobiotus richtersi in ten of their three hundred thirty-eight samples. According to their collection data, seven of these samples were mosses, two were lichens, and one was forest litter; yet, in their text they state ..."all but one of the specimens were from very damp moss." They also stated that Macrobiotus richtersi is a large animal reaching about 1,000u in length, but did not give an average or a range of measurements for their specimens. They stated the color may vary from white through a brownish hue. The substrate of the plants yielding this species was varied; two from soil, four from trees, one from a rock, and three unrecorded.

Western Montana yielded sixteen samples with Macrobiotus richtersi; fourteen were mosses, one was a lichen, and one was a vascular plant. The favored substrates that these plants inhabited were rock and soil with six samples collected from each; of the remainder, one was a tree

and three were fallen logs.

The specimens from Montana had a size range from 370u to 620u, well below the range reported by Puglia (1959) in Illinois, and not reaching the limit of 1,000u suggested by Schuster and Grigarick (1965). These measurements do fit well within the range reported by Riggin (1962) of 232u to 759u.

All reported color ranges, colorless thru white to a light brown, were observed in the animals from Montana.

Three-fifths of the samples containing Macrobiotus richtersi were dry, not "very damp" as reported by Schuster and Grigarick (1965).

Macrobiotus richtersi is known from Germany, France, Scotland, Ireland, Sweden, Africa, Samoa, Yugoslavia, Czechoslovakia, Greenland, Spain, Austria, Italy, and the United States (Riggin, 1962).

Genus Hypsibius Ehrenberg, 1848

> "Char. Generis: Corpus non scutatum, nudum, annulatum. Annuli corporis alterni pedibus instructi. Pedum paria 4. Os breviter tubulosum cum capite non apprendiculatum. Manidbulae inclusae duae. Occuli nulli."

The genus Hypsibius is characterized by the paired claws of each leg being of different sizes, structures, or shapes. The outer claw is larger than the inner claw. Cuticle may be smooth, spiny, or papillose. Eyespots may be present. The buccal tube is narrow, lacking apodeme support. The pharyngeal tube may be longer than buccal tube. The stylets are slight, with supports present, furcae are reduced. Pharynx may be oval, or spherical. The macroplacoids are present in varying shapes and numbers. Microplacoid may be present or absent. Septulum may be present.

The genus Hypsibius is divided into four subgenera: Isohypsibius, Hysibius, Diphascon, and Calohypsibius.

Subgenus Hypsibius (Isohypsibius) is characterized by claws that have both branches separated at the base, independently, and at right angles to each other. Cuticle may be smooth or papillose. Two or three macroplacoids may be present. Microplacoid may be present or absent. The buccal tube is longer than the pharyngeal tube. The pharynx may be spherical to slightly oval.

Subgenus Hypsibius (Hypsibius) is characterized by the secondary branch of the external claw forming a right angle. The cuticle may be smooth or papillose. The buccal tube is longer than the pharyngeal tube. Two macroplacoids are present. A microplacoid may be present or absent. Pharynx is spherical to slightly oval.

Subgenus Hypsibius (Diphascon) is characterized by claw differences. The secondary branch of the outer claw is thick, whereas the primary branch tends to be thin. The pharyngeal tube is long and thin, longer than half the length of the pharynx. The pharyngeal tube is flexible, often convoluted. The buccal tube is short and narrow. The stylets and stylet supports are small and thin. Pharynx is oval, sometimes elongated oval. Two or three macroplacoids may be present. Microplacoid may be present or absent, as might a septulum.

Subgenus Hypsibius (Calohypsibius) is characterized by a weakly sclerotized area between the branches of the external claws. Only a single specimen representing this genus has been reported from North America, by Schuster and Grigarick (1965) from Popof Island in Alaska.

Nine different species representing three of four subgenera were collected and identified during this study.

Hypsibius (Diphascon) alpinus (Murray, 1906)

> "Specific characters. - Whitish, narrow, of nearly equal width throughout. Teeth curved, divergent; gullet slender, very long. Pharynx broad, oval, or thromboid, short diameter to long as 8 to 11; 3 rods in each row increasing both in length and thickness from first or third. The claws, a larger and a smaller pair, one claw of each pair longer and with a supplementary point. The claws are thicker than in the other species, the larger claw of the smaller pair especially. Length over all 250u."

Hypsibius (Diphascon) alpinus from Montana

Nine specimens of Hypsibius (Diphascon) alpinus were collected from western Montana. Average length 182u, excluding legs IV, range of measurements from 108u to 246u. Cuticle smooth, eyespots absent. Claws typical of the genus Hypsibius. Pharyngeal tube thin, buccal apparatus small, pharynx slightly oval. Apophysis, three macroplacoids, a microplacoid present. Macroplacoid size increasing, first to last. All macroplacoids smooth and roundish, in neat rows. Microplacoid angular, curving toward center. Pharyngeal tube about three times length of pharynx.

Hypsibius (Diphascon) alpinus in North America

First described by Murray (1906) as Diphascon alpinus from Scotland, Hypsibius (Diphascon) alpinus was first reported in North America by Murray (1910) from the Rocky Mountains of Canada.

Schuster and Grigarick (1965) published the first report of the animal in the United States. However, it was collected at only three of two hundred nineteen sites, one each in Nevada, Washington, and Alaska.

It should be noted that this species did not appear in Riggin's (1962) work in Virginia, in Puglia's (1959) work in Illinois, or in Higgins' (1959) work in Colorado.

Nine specimens of Hypsibius (Diphascon) alpinus were recovered from western Montana during this study.

Hypsibius (Diphascon) alpinus, ecology notes.

Schuster and Grigarick (1965) removed this species from a sample of bog, a sample of moss, and a sample of moss and lichen on a rock.

The four collection sites in western Montana were all in the Flathead River drainage. All four samples were mosses which were found on a soil substrate and were moist at the time of collection. In the cases of the three mosses that were identifiable, each was the only sample of that species of moss which were collected during this study.

Schuster and Grigarick (1965) stated that the animal is cosmopolitan.

Macrobiotus hufelandii occurred in each sample from which Hypsibius (Diphascon) alpinus was extracted; Macrobiotus harmsworthi occurred in three of the four samples; Macrobiotus richtersi, Macrobiotus islandicus, Hypsibius convergens, and Pseudechiniscus raneyi

also occurred in one sample together.

The lack of occurrence of this species in the collections in the eastern United States creates a disjunct distribution for a "cosmopolitan" animal. If the animal is indeed absent from the intervening areas, the most obvious answer is lack of habitat. H.S. Conrad's book How to Know the Mosses and Liverworts tends to support this habitat theory, as Hypsibius (D.) alpinus has been collected from the following plants:

> Pseudoleskea patens (Lindb.) Limpr. is reported to occur from Newfoundland to British Columbia, California, Idaho and New Hampshire.
>
> Rhytidiopsis robusta (Hook) Broth. is a plant of the northwest, east to Montana.
>
> Leptodictyum riparium (Hedw.) Warnst. no distribution is given.

Hypsibius (Diphascon) alpinus has been reported from British Columbia, Washington, Nevada, Alaska, and Montana. No correlation can be drawn from so little data, but this is the first positive indicator that there may be an association between plant and animal. The distribution of particular mosses may define the distribution of particular tardigrades.

Hypsibius (Diphascon) angustatus (Murray, 1905)

> "Specific Characters. - Large hyaline, broadest about third legs, thence tapering to the narrow snout-like head. Pharynx narrow, twice as long as broad; two slender rods in each row-first short, second twice as long. Gullet very short and wide, marked by annular rings, very slightly flexible. Mouth and throat wide. Teeth straight, only slightly divergent, with or without small weak bearers. Claws two unequal pairs, one pair with one claw long and slender.

Distinguished from D. spitzbergense by the general form, tapering anteriorly, the shorter wider gullet, still narrow pharynx, and number of pharyngeal thickings.

Habitat. - Loch Ness, February 1904. Common. Richters has also observed this species in Germany.

Hypsibius (Diphascon) angustatus from Montana.

One specimen of Hypsibius (D.) angustatus was collected in western Montana. Length 425u, excluding legs IV. Cuticle smooth, eyespots absent. Claws typical of the genus Hypsibius. Esophageal tube stout, thick, with short stylet supports. Pharyngeal tube short, thick, annulate, Two macroplacoids, no microplacoid. Second macroplacoid twice as long as first, macroplacoids thin, pointed on non-joining ends, lance-like.

Hypsibius (Diphascon) angustatus from North America.

Named Diphascon angustatus by Murray (1905), the first collection of this species from North America was by Riggin (1962) from Virginia. Riggin followed the scheme of classification and continued the generic status of Diphascon. Ramazzotti (1962) placed Diphascon in a subgeneric status and this classification has been followed since.

Riggin (1964) reported the second record of Hypsibius (D.) angustatus from North and South Carolina.

Schuster and Grigarick (1965) examined a few specimens from California, Oregon, and Washington.

Hypsibius (Diphascon) angustatus, Ecology notes

Moss was reported present in all of the samples which contained Hypsibius (D.) angustatus (Schuster and Grigarick, 1965).

A single example of Hypsibius (D.) angustatus was collected from western Montana. This individual was collected from the Bitterroot drainage and was the only animal found in the only sample of the moss Pogonatum alpinus during this study. The moss was moist and growing on a soil substrate.

Hypsibius (Diphascon) arduifrons (Thulin, 1928)

> "Korper hinten dick, vor dem zweiten Beinpaare sich nach vorn stark verjungend. Vorderkopf dorsal von der schief nach unten gerichteten Mundoffnung vorgewolbt.
> Augen fehlen. Mundrohre sehr dunn, ihr mittlerer Teil gleich lang wie der grosse, gestreckt eiformige Pharynx. Placoidenreihen langer als die halbe Schlundkopflange, jede drei dunne Stabchen enthaltend, von denen das kleinste vorn, das grosste hinten gelegen ist. Microplacoiden fehlen, Apophysen dagegen vorhanden. Krallen wie bei der vorigen Art.
> Dimensionen. - Korperlange 284u. Pharynxlange 35.9u-126ms. Hinterkralle IV 12.8u=45ms. Krallenlangenindes 1.50 : 1.
> Ausserer Durchmesser der Mundrohre 4.7 cph. Mundring + vorderer Abschnitt der Mundrohre (siehe unter D. Tenue!) 45 cph; mittlerer Abschnitt der Mundrohre 99 cph. Pharynxbreite 55 cph. Placoidenreihe 55 cph. Placoiden resp. 13.7, 14.7, und 22.5, ihre Breite 2.7 cph."

Hypsibius (Diphascon) arduifrons from Montana.

Nine specimens of Hypsibius (Diphascon) arduifrons were collected in western Montana. Average length 219u, excluding legs IV, range of measurements 182u to 259u. Cuticle smooth, eyespots absent. Mouth sub-terminal. Buccal tube straight. Stylets close to buccal tube. Stylet supports angular, attaching anteriad to base of buccal

tube. Pharyngeal tube long, thin, angular, bending more than ninety degrees before entering pharynx. Pharynx oval, elongated. Apophysis present. Three macroplacoids present. Macroplacoids increasing in size, anteriad to posteriad. Microplacoid absent. Septulum absent. Third macroplacoid longest, first shortest. Macroplacoids smooth, rod shaped. Claws typical of the genus Hypsibius, unequal in length. The color of the specimens was white.

Hypsibius (Diphascon) arduifrons from North America.

This report constitutes the first record of this species of tardigrade from North America.

Hypsibius (D.) arduifrons has been collected from Bohemia, Italy, Lapland, and Siberia (Ramazzotti, 1962).

Identification was based on Ramazzotti's (1962) description.

> "Small size (length about 285u), cuticle smooth, eyes absent...The buccal aperature turned obliquely towards down, (subventral) at front...
> Buccal tube very narrow (less than 1.5u in an individual 284u long), pharyngeal tube (flexible) long, about as the bulb, with the form of an elongated egg. Apophysis visible with three macroplacoids, with shape of a thin cane, length decreasing from first to third; microplacoid absent; longest of the single fire is the third macroplacoid." (Translated from the Italian by me).

Two examples of this species were sent to Robert O. Schuster, Senior Scientist, University of California, Davis, for confirmation. Mr. Schuster confirmed the identification as Hypsibius (Diphascon) arduifrons.

Hypsibius (D.) arduifrons, ecology notes.

Hypsibius (D.) arduifrons was collected from two sites in the upper portions of Rock Creek, a tributary to the Clark Fork Drainage. Both samples of moss were dry at the time of collection. Both samples were collected the same day.

Hypsibius (Diphascon) oculatus (Murray, 1906)

> Specific characters. - Large, narrow, broadest in middle. Two dark eye-spots. Teeth curved, with bearers; gullet very long, slender; pharynx nearly round; thickenings two short oval bodies and at posterior end a little round nut (what Richters calls a "Komma"). Claws, a short thick pair, and a pair with one very long claw apparently springing from the middle of the back of the shorter claw, long claw with a fine spine near the apex.

Hypsibius (Diphascon) oculatus from Montana.

Four specimens of Hypsibius (D.) oculatus were collected in western Montana. Average length 221 u, excluding legs IV, range of measurements from 191u to 233u. Cuticle smooth, colorless or opaque white. Eyespots present. Mouth subterminal. Annulate pharyngeal tube twice as long as slightly oval pharynx. Two macroplacoids present, first larger than second, both irregularly shaped. Microplacoid present. Apophysis present. Buccal tube one-third to one-fourth length of pharyngeal tube. Buccal tube defined by stylet supports. Accessory sack present, immediately below stylet supports, attached to pharyngeal tube.

Hypsibius (Diphascon) oculatus from North America.

Hypsibius (D.) oculatus was first described by Murray (1906) from Vancouver Island, British Columbia. The form Diphascon canadense was placed in synonomy with Hypsibius (D.) oculatus by Murray in 1910.

Schuster and Grigarick (1965) made the first report of this species from the United States. Nearly two hundred specimens were collected from California, Oregon, and Washington.

The four examples of Hypsibius (D.) oculatus from western Montana constitute the fourth report of this animal from North America.

Schuster and Grigarick (1965) reported maximum length of 400u for Hypsibius (D.) oculatus. They also stated that a septulum was present, as were eyespots. No mention is made of an accessory sac found at the end of the buccal tube below the stylet supports, yet it is indicated in their drawings.

The four examples of this species from western Montana lack eyespots, have microplacoids, not a septulum as reported by Schuster and Grigarick (1965), and an accessory sac is present.

Hypsibius (Diphascon) oculatus, ecology notes.

Schuster and Grigarick (1965) found Hypsibius (D.) oculatus in thirty-eight samples. Twenty-eight of these samples contained lichens, and trees were the substrate in twenty-four of the samples.

All the specimens from Montana were removed from samples of mosses. Three were from a rock substrate, one was from a soil substrate.

Hypsibius (D.) oculatus has been found only in the Pacific Northwest drainages. Higgins (1959) did not report this species from

Colorado. Schuster and Grigarick (1965) did not find Hypsibius (D.) oculatus in collections from either Arizona or Alaska.

Hypsibius (D.) oculatus is also known from Europe.

Hypsibius (Diphascon) scoticus (Murray, 1905)

> "Specific characters. - Large, hyaline. Teeth curved widely divergent, with bearers. Gullet long, slender, flexible portion about as long as the pharynx. Pharynx narrow, twice as long as broad, slightly narrower in front, thickenings four in each row, the first two elongate rods of equal size, the third a similar but longer rod, the fourth a small nut. Claws, a long and a short in each pair, the long claw of one pair much longer than that of the other. Like D. angustatum in the narrow pharynx, it differs in having twice as many thickenings in each row and in the long slender gullet. The general form is also different, lacking the decided anterior narrowing of D. angustatum. Size, up to 1/66 inch=378u. Otterston, near Aberdour, Fife, March 1905 (W. Evans); and in moss, Boltonmoore, East Lothina, April. Since found in several localities outside of the Forth Valley."

Hypsibius (Diphascon) scoticus from Montana.

Six specimens of Hypsibius (Diphascon) scoticus were collected in western Montana. Average length 139u, excluding legs IV, range of measurements 106u to 187u. Cuticle smooth, eyespots absent. Three macroplacoids, a microplacoid present. Second macroplacoid shortest. Third macroplacoid longest. Macroplacoid thin to blocky, not globular. Small apophysis present. Microplacoids longer than wide, posterior angled toward center. Claws typical of the genus Hypsibius, unequal. Buccal tube one-fourth length of pharyngeal tube. Pharyngeal tube longer than pharynx. Stylet supports straight.

Hypsibius (Diphascon) scoticus from North America.

Murray (1910) reported Hypsibius (D.) scoticus from Vancouver, British Columbia, and the Rocky Mountains of Canada. Higgins (1959) found the first examples of this species in the United States near Boulder, Colorado. Riggin (1962) reported a single specimen from Virginia.

Schuster and Grigarick (1965) reported finding Hypsibius (D.) scoticus in California, Oregon, and Washington.

Six examples of this species were recovered and studies from western Montana during this study.

Hypsibius (D.) scoticus, ecology notes.

Higgins (1959) found four specimens of Hypsibius (D.) scoticus in the same locality as M. islandicus, but did not say the species were in the same sample, nor was the habitat reported in which Hypsibius (D.) scoticus was found. Higgins reported the color of the animal as "brownish-gray." "The mouth appears subterminal; three macroplacoids were barely distinguishable." (Higgins, 1959). His drawings failed to clarify the arrangement and relationships of the mouth parts.

Riggin (1962) reported from one specimen that the anterior macroplacoid was the shortest. Riggin described the "elongated-oval spetulum." This individual measured 243u in length. No ecological information about the animal was reported.

Schuster and Grigarick (1965) reported Hypsibius (D.) scoticus from eleven collection sites on the west coast. These animals ranged

in length from 210u to 390u. Schuster and Grigarick reported that of the three macroplacoids, the middle macroplacoid is normally the shortest. They further stated that the septulum is absent. Their drawings indicate differences in the thickness of the macroplacoids.

Schuster and Grigarick reported Hypsibius (D.) scoticus from five samples of lichens, four samples of mosses, and one sample of a moss-lichen combination. Trees were the substrate in four samples, and soil was found in four samples.

The examples of Hypsibius (D.) scoticus which were found in western Montana closely match the description and drawings of Schuster and Grigarick (1965). Riggin (1962) reported a septulum, which was not present in the animals from Montana. It was reported absent by Schuster and Grigarick (1965). Riggin determined the first macroplacoid to be the shortest. Conversely, the specimens which were collected by Schuster and Grigarick and those found in Montana do not fit this description. The second macroplacoid of these specimens was the shortest.

Hypsibius (D.) scoticus was found in five samples of mosses, all of which were different species, on soil, tree, and fallen log substrates. One of these samples was taken from the sphagnum bog of McGee's Meadow in Glacier National Park. The pH of the interstitial water at McGee's Meadow was 3.5 the day the sample was taken. The Hypsibius (D.) scoticus that was recovered from this sample was the only tardigrade found in the sample.

Tardigrades were reported by Fantham and Porter (1945) from two species of Sphagnum moss out of the eighteen species of Sphagnum

which were examined. Unfortunately, Fantham and Porter did not report the species of the tardigrades which were found. Sphagnum girgensohnii Rowdon, and Sphagnum capillaceum Lantier, were the two species reported to have yielded tardigrades.

Hypsibius (D.) scoticus has been reported from Scandinavia, Germany, rance, Czechoslovakia, Italy, United States, Scotland, Ireland, China, Hawaii, Australia, Vancouver Island, Canada, South America (Riggin, 1962).

Hypsibius (Diphascon) spitzbergensis (Richters, 1903)

The original description is not available.

Hypsibius (Diphascon) spitzbergensis from Montana.

Three specimens of Hypsibius (D.) spitzbergensis were collected in western Montana. Average length 415u, excluding legs IV, the range of measurements 355u to 475u. Cuticle smooth, eyespots absent. Claws typical of the genus Hypsibius, unequal. Pharyngeal tube long and annulate, pharynx elongated, oval. Two macroplacoids present. Macroplacoids long, thin, the first macroplacoid one-half length of the second macroplacoid. Microplacoid present. Microplacoid pointed posteriad, points converging. Stylet supports one-third of distance from mouth to pharynx.

Hypsibius (D.) spitzbergensis from North America.

Schuster and Grigarick (1965) found a single example of this species on the west coast. This individual was collected from "lichen on moss on bark and twigs."

The three specimens of Hypsibius (D.) spitzbergensis which were found in Montana constitute the second report of this animal from North America.

Hypsibius (D.) spitzbergensis is also known from Europe and the Arctic. (Schuster and Grigarick, 1965).

It should be noted that two equally uncommon species, Hypsibius (D.) spitzbergensis and Echininscus quadrispinosus, were removed from the same sample of moss. Macrobiotus areolatus occurred in another sample with Hypsibius (D.) spitzbergensis, whereas only two other individuals of either animal were collected. Macrobiotus hufelandii occurred in every sample in which Hypsibius (D.) spitzbergensis was found.

Schuster and Grigarick (1965) reported Hypsibius (D.) spitzbergensis with the following tardigrades in the same sample: Macrobiotus hufelandii, Macrobiotus islandicus, Hypsibius scoticus, Hypsibius oberheauseri, and Milnesium tardigradum.

Hypsibius (Hypsibius) convergens (Urbanowics, 1925)

"1) Z wyranznemi czarnemi oczami.
Przewod gardzielowy zakonczony trojkatnemi apofizami.
Gardziel owlana (dl. 24u, szer. 18u).
Stosunek dlugosci gornego rzedu precikowatych zgrubien wewnatrz gardzieli do dolnego rzedu jak 3 : 2.
Najdtuzszy pazur potaczony z sasiednim na 1/3 jego wyxokosci; dwa pozostate rowniez niejednostajnej dtugosci zrosniete sa na znacznej przestrzeni.
Dtugosc ciata do 300u.
Jaja okraglt od 45-54u."

Hypsibius (Hypsibius) convergens from Montana.

Forty-four specimens of Hypsibius (Hypsibius) convergens have

been collected from western Montana. Average length 226u, excluding legs IV, range of measurements 156 to 301u. Cuticle smooth, eyespots present. Broad pharyngeal tube, round pharynx. Large apophysis. Two macroplacoids, no microplacoids. Macroplacoids globular or elongate, not smooth or round. Mouth subterminal. Stylet supports wide, straight and flat. Outer claw primary branch tapering to base.

Hypsibius (Hypsibius) convergens from North America.

Hypsibius (H.) convergens was first reported from North America by Murray (1907), but no collection site was noted. Marcus (1928) listed a collection of this species from Niagara Falls, New York. Riggin (1962) reported the animal from Virginia.

Schuster and Grigarick (1965) assigned about one hundred specimens from California, Oregon, and Washington to this species.

Forty-four specimens of Hypsibius (H.) convergens have been collected from western Montana.

Hypsibius (H.) convergens, ecology notes.

Riggin (1962) reported sixteen specimens ranged in length from 151u to 276u; no ecological information was included. Schuster and Grigarick (1965) considered Hypsibius (H.) convergens of moderate size somewhat over 400u but usually less. Of their forty-two samples: twelve were lichens, sixteen were mosses, nine were moss-lichen combinations, and five were other things or not reported. The reported substrates on which Schuster and Grigarick (1965) found plants bearing this species were soil, seven samples; rock, eight samples; trees, fourteen samples; undefined, thirteen samples.

Hypsibius (H.) convergens was found in fourteen samples throughout western Montana; ten of these samples were mosses, two were lichens and two were vascular plants. Soil was the substrate found in six samples, rock was found in four samples, and trees were found in two samples.

Hypsibius (H.) convergens has been collected from: Greenland, Iceland, Scandinavia, Germany, France, Spain, Scotland, Czechoslovakia, United States, Brazil, and Italy (Riggin, 1962).

Hypsibius (Hypsibius) oberhaeuseri (Doyere, 1840)

The original description is not available.

Hypsibius (Hypsibius) oberhaeuseri from Montana.

Thirty-four specimens of Hypsibius (Hypsibius) oberhaeuseri were collected in western Montana. Average length 274, excluding legs IV, range of measurements from 187 to 394u. Cuticle may appear smooth, actually granular. Cuticle pigmented in five longitudinal and nine transverse bands. Color, red or brown in bands, white between bands. Ventral surface and legs without color. Claws different sizes, outer with primary branch long, thin, base not much wider than tip. Secondary branch strongly recurved. Inner claw branches short, stubby. Pharyngeal tube narrow, pharynx slightly oval or round, large. Apophysis present. Two macroplacoids round, near equal in size. Macroplacoids smooth. Microplacoid and septulum absent. Stylet supports attach at mid-point on pharyngeal tube.

Hypsibius (Hypsibius) oberhaeuseri from North America.

Murray (1910) found Hypsibius (H.) oberhaeuseri on Vancouver Island, British Columbia. Mathews (1938) reported collecting this species from Santa Catalina Island, California, and East Troy, Wisconsin.

Puglia (1959) collected Hypsibius (H.) oberhaeuseri from Illinois. Baumann (1960) found this species in Colorado, and Higgins (1960) reported it from North Caolina. Riggin (1962) collected two specimens in Virginia.

Schuster and Grigarick (1965) recorded Hypsibius (H.) oberhaeuseri from Arizona, California, Oregon, and Washington.

This is the first record of this species reported from Montana.

Puglia (1959) reported a length of less than 500u, Schuster and Grigarick (1965) reported a length of slightly over 400u. Riggins (1962) reported only two specimens with length of 193u and 234u. The animals from Montana range from 187u to 394u and average 274u.

Hypsibius (H.) oberhaeuseri, ecology notes.

Puglic (1959) found Hypsibius (H.) oberhaeuseri in seven samples; all were lichens. Riggin (1962) did not report the habitat in which two examples of this species were found.

Schuster and Grigarick (1965) found Hypsibius (H.) oberhaeuseri in eighty-one samples from seventy-three collection sites. Fifty-three of these samples were lichens, eleven were moss-lichen combinations, and eighteen were mosses. Trees were the substrate reported in fifty-three of these samples.

Moss was the habitat in seven of the eleven samples from Montana which yielded Hypsibius (H.) oberhaeuseri. Lichens were the habitat in only three of the eleven samples. Rocks were the substrate in five samples, soil in two samples, and trees in two samples.

Hypsibius (Hypsibius) oberhaeuseri has been reported from: Scandinavia, Germany, France, Spain, Portugal, Czechoslovakia, Africa, Sandwich Island, British Columbia, Brazil, Columbia, Greenland, United States, Italy, and Palestine (Riggin, 1962).

Hypsibius (Isohypsibius) prosostomus (Thulin, 1928)

> "Aus oben (p. 247) angegebenem Grunde schlage ich fur diese Art einen neuen Namen vor. Sie steht I. Schaudinni und I. canadensis nahe. Von dem ersteren unterscheidet sie sich durch die Form des Kopfes, indem die Mundoffnung bei I. Schaudinni mehr nach unten, bei I. prosostomus mehr nach vorn gerichtet ist, sowie durch viele Einzelheiten des Buccalapparates-geradere Mucdrohre, mehr Form des Schlundkopfes, verhaltnismassig langere Macroplacoidenreihen (41 cph bei I. p., 34 cph bei I.S.), gestrecktere Placoiden, Vorhandensein eines Microplacoids etc. Von dem viel kleineren I. canadensis differient sie durch den ovalen Pharynx, die weite Mundrohre, anscheinend auch durch die Proportionen der Placoiden und vielleicht durch grobere Krallen."

Hypsibius (Isohypsibius) prosostomus from Montana.

A single specimen of Hypsibius (Isohypsibius) prosostomus was collected in western Montana. Length 274u, excluding legs IV. Cuticle smooth, eyespots present. Buccal tube stout. Stylet supports wide. Pharyngeal tube short, apophysis present. Three macroplacoids present. Microplacoid present. Macroplacoids increasing in size, first to third. Pharynx slightly oval. Claws typical of Isohypsibius, secondary branch forming right angle to main axis.

Hypsibius (Isohypsibius) prosostomus from North America.

Mathews (1938) reported this species from Isle Royal, Michigan. Schuster and Grigarick (1965) recovered Hypsibius (I.) prosostomus from eight sites in California.

Schuster and Grigarick (1965) reported lengths up to 500u and eyespots as not always present.

Hypsibius (Isohypsibius) prosostomus, ecology notes.

Hypsibius (Isohypsibius) prosostomus were recovered from samples of mosses, lichens, moss-lichen combinations, and from soil, rock, and tree substrates. No habitat or substrate dominated the collections of Schuster and Grigarick (1965)

The single example from Montana came from a moss with a rock substrate.

Hypsibius (Isohypsibius) prosostomus has been reported from Europe, Indonesia, and the United States. (Schuster and Grigarick, 1965).

Genus Milnesium Doyere, 1840

"tete portant a sa partie anterieure et laterale duex appendices palpiformes tres courts; bouche terminee par une ventouse entouree de palpes.
Peau molle, coupee transversalement par des sillons, en anneaux de formes variables.
Quatre paires di pattes.
Anneaux du tronc bisegments.
Aucune trace di metamorphoses.
En dediant ce genre a M. Milne Edwards, c'est un hommage que j'ai voulu rendre au savant, qu'un temiognage de ma reconnaisance pour l'homme auquel je dois tout: et j'ai choisi de preference l'espece qui m'a fourni le plus d'elemns de succes, parcr que j'ai cru lui dedier ainsi mon travail tout entier."

The branches of the claws are completely separated, one being long and think the other short and stout with three hooks or branches. Six papillae surround mouth, two lateral papillae on head. Buccal tube is wide. The stylets are small and parallel to the buccal tube. The pharynx is elongated and without placoids.

The family Milnesidae is monotypic.

Milnesium tardigradum Doyere, 1840

> "Bouche entouree de six petits palpes inegaux disposes symetriquement, decroissant de la partie superieure a la partie infetriquement, decroissant de la partie superieure a la partie inferieure; un en dessus plus grand, un dessous tres petit, situes dans le plan median.
>
> Tete arrondie en avant lorsque le museau est rantre; points oculiformes assex grands, granuleux. Tube pharyngien tres dilate; stylets tres petits, bulbe allonge, pyriforme, sans charpente interieure.
>
> Corps transparent, plus attenue a ses deux extremites et surtout a la posterieure, que dans aucune des autres especes.
>
> Sang incolore.
>
> Peau legerement coloree en brun-jaune.
>
> Membres, les trois paires anterieures a-peu-pres egales, la posterieure tres courte, ne ressemblant plus qu'a deux mamelons presque sans traces de divisions annuliforems.
>
> Ongles au nombre de quatre a chaque patte, dont deux terminaux simples et en forme de filamens allonges chochus a l'extremite, portes chaucun sur un mamelon distinct; deux situes en dessous et en dedans, l'anterieur divise en trois crochets fortement courbes, le posterieur en deux. Les ongles on filamens terminaux de la quatrieme paire sont plus longs que ceux des trois premieres.
>
> Cette espece habite la mousse des toits. Elle est abondanta a Saint-Maur."

Milnesium tardigradum from Montana.

Five specimens of Milnesium tardigradum were collected in western Montana. Average length 518u, excluding legs IV, range of

measurements 259u to 844u. Cuticle smooth, eyespots present. Six papillae ring large mouth. Buccal tube wide. Stylets short, in sheaths juxtaposed to buccal tube. Stylet supports short. Pharyngeal tube absent. Pharynx pear shaped, originating from base of buccal tube. Pharynx without placoids. Claws unequal, primary claw long, thin, tip hooked, on separate conical "toes" unbranches. Basal claw stout, short, three hooked branches. Color light brown.

Milnesium tardigradum in North America.

Murray (1910) found Milnesium tardigradum on Vancouver Island, British Columbia. Mathews (1938) reported finding this species in Wisconsin, Washington, and Illinois. Curtin (1957) found two examples in Maryland.

Puglia (1959) reported Milnesium tardigradum from Illinois. Higgins (1959) and Baumann (1960) collected this species in Colorado. Higgins (1960) recovered examples from North Carolina. Riggin (1962) examined several specimens of Milnesium tardigradum from Virginia.

Riggin (1964) wrote of a single specimen from South Carolina. Schuster and Grigarick (1965) reported over five hundred specimens of this species from Arizona, California, Idaho, Nevada, Oregon, and Washington.

Five specimens of Milnesium tardigradum were collected from western Montana during this study.

Milnesium tardigradum comparisons.

Riggin (1962) reported thirty specimens which ranged in length from 304u to 908u. Puglia (1959) reported lengths up to 1,025u.

Schuster and Grigarick (1965) did not report length.

Higgins (1959) described the body of Milnesium tardigradum as "shrew-like", tapering to the front. Both Higgins (1959) and Puglia (1959) reported the color of this species to be red or brownish. Schuster and Grigarick (1965) reported the color to vary from transparent to pinkish white. The Montana examples were light brown in color.

Milnesium tardigradum ecology notes.

Higgins (1959) reported Milnesium tardigradum from moss. Puglia (1959) found this species in thirty lichen samples, eleven moss samples, four forest litter samples, and four samples of grass. Riggin (1962) reported that one of the samples in which Milnesium tardigradum was found was a moss. He postulated that this sample had been submerged prior to its collection. This indicates a possible aquatic occurrence for this animal.

Schuster and Grigarick (1965) states, "It seems equally abundant in xeric conditions of the valley areas of California or in the moist north coastal regions. It has been recovered from moss and lichen, but never from aquatic samples." Milnesium tardigradum was found in one hundred forty-three samples by Schuster and Grigarick; ninety-two of those samples were lichens, twenty-six were mosses, fourteen were moss-lichen combinations, and eleven were other habitats.

The five specimens from Montana were collected from three different species of mosses, from three different sites.

Pennak (1953) stated that Milnesium tardigradum is chiefly carnivorous. During this study, a specimen, later identified as Milnesium

tardigradum, was observed attached to the midsection of a nametode. The nematode was over five times the length of the tardigrade, and exhibited extremely violent whipping and wiggling actions, and carried the tardigrade to the extremes of the stender dish in which they were contained. After about five minutes, the violent action of the nematode decreased. At the end of nine minutes, the tardigrade had transferred to a moss substrate. The nametode was motionless.

Milnesium tardigradum is the most widely distributed tardigrade in North America. It is also known from: Greenland, Spitzbergen, Scandinavia, Scotland, Ireland, Germany, France, Yugoslavia, Spain, Portugal, Czechoslovakia, Italy, West Africa, Sumatra, Java, Hawaii, Australia, Canada, United States, Brazil, Columbia, Chile, Paraguay, and Japan (Riggin, 1962).

Genus Echiniscus Schultz 1840

> Genus: Echiniscus. Corpus ovato-elongatum. scutatum, spinosum. in novem segmenta distinctum, pedes octo alternis segmentis a terio ad nonum affixi. Caput antennis quatuor spinisque duabus instructum, oculi simplices duo.

This genus is characterized by the presence of five dorsal plates. The terminal plate E is directly behind plate D or separated from D by one or two intersegmental plates. A lateral spine is present at A and may be present at other positions. The four claws of each leg arise independently.

The plates are lettered A to E from anteriad to posteriad (see plate II). The area between these plates is intersegmental and may contain plates which are numbered 1 to 3 anteriad to posteriad. Spines

which originate on the plates and atop the animal are called dorsal spines and are lettered for the plate from which they originate. Lateral spines arise near the posterior, later edge of the plate and are lettered accordingly.

Plate E may have a furrow or incision in its posterior surface which is labeled G. This furrow may have a small spine, not considered a lateral, and is labeled F.

Buccal spines or cirri are internal or external depending on whether they are anteriad or posteriad to the buccal papilla. Another papilla or clava K may be present at the base of spine A. (See plate 1, fig. A.).

About ninety-five species, subspecies, and varieties of Echiniscus have been proposed. Three species were collected from western Montana.

Echiniscus (Echiniscus) arctomys Ehrenberg, 1853

The original description is not available.

Echiniscus (Echiniscus) arctomys from Montana.

Three specimens of Echiniscus (E.) arctomys were found in western Montana. Average length 154u, excluding legs IV, range of length measurements from 124u to 191u. Eyespots present. Dorsal plate sculpture even, not patterned, Median plate #3 absent, cuticle between plates D and E sculptured. Only lateral spine A present. Inner claws with spurs. Collar of leg IV with two sizes of teeth.

Echiniscus (Echiniscus) arctomys from North America.

Mathews (1938) reported several specimens from Vermont and

Wisconsin. Riggin (1962) included Echiniscus (E.) arctomys from North America.

The three specimens collected during this study were all from the same moss sample. This was one of two incidences of this species of moss during the study.

Eichiniscus (Echiniscus) quadrispinosus Richters, 1902

Original description is not available.

Echiniscus (Echiniscus) quadrispinosus from Montana.

Two specimens of Echiniscus (Echiniscus) quadrispinosus were collected in western Montana. Measured lengths were 157u and 187u, excluding legs IV. Eyespots absent. Inner claws with spurs, outer claws smooth. Dorsal plate sculpture irregular, pitted, Lateral spines present at A, C, D, and E. Absent at B. Lateral spines moderate in length. Dorsal spines short, present at C and D. All dorsal plates present. One transverse area on dorsal plate B without pattern, smooth. No noticeable collar on Legs IV.

Echiniscus (Echiniscus) quadrispinosus from North America.

Schuster and Grigarick (1965) reported the first collection of Echiniscus (E.) quadrispinosus from North America with a single specimen from California.

The collection of this species from Montana constitutes the second record of Echiniscus (E.) quadrispinosus from North America.

Echiniscus (Echiniscus) quadrispinosus ecology notes.

Schuster and Grigarick (1965) found their single individual in a sample of moss at the confluence of the Scott and Klamath Rivers in northern California.

In Montana, one specimen was removed from each of two different mosses. One of the samples also yielded Hypsibius (D.) spitzbergensis, an animal of which only four individuals are known from North America.

Echiniscus (Echiniscus) trisetosus Cuenot, 1932

> "L'unique difference entre trisetosus (fig. 31) et Blumi porte sur la disparition du filament B, de sorte qu'il ne reste que les filaments A, C et D (d'ou le nom de trisetosus que je donne a cette forme, pour remplacer celui de granulatus qui lui a ete attribue a tort par tous les auteurs). Le passage a Blumi est etabli par un individu asymetrique, figure par Marcus, qui presente d'un cote seulement un piquant B. - Ponte dans la mue de 2 a 5 oeufs; la larve a 2 griffes que l'on peut rapporter a cette forme presente C et D courst et les appendices dorsaux.
>
> La variation est intense; j'ai vu plusieurs fois C bifide d'un cote, simple di l'autre; C, D et Dd peuvent etre de longs piquants et non plus des filaments; Dd, qui est habituellement court, est parfois rudimentaire ou manque d'ordinaire, peut etre un court spicule triangulaire, parfois un piquant assez long (les exemplaires ecossais vus par Murray ont constamment un long spicule E). L'asymetrie (fig. 30) est frequente, un appendice pouvant etre long d'un cote et court de la'autre, ou pouvant meme manquer d'un dote. Les eperons des griffes externes du pied IV sont parfois doubles et meme triples, le proximal etant plus grand que les autres. Toutes ces variations se recontrent dans la meme Mousse avec des trisetosus parfaitement typiques."

Echiniscus (Echiniscus) trisetosus from Montana.

One specimen of Echiniscus (Echiniscus) trisetosus was found in western Montana. Length 157u, excluding legs IV. Eyespots absent. Dorsal plate pattern irregular, weak between plates. Claws with spur, outer claw spur recurved, inner claw spur straight. Collar of leg IV

serrate, teeth near equal. Lateral spines present at A, C, and D. Dorsal spines present at C and D. Dorsal spine C long, dorsal spint D short. Lateral spines long.

Echiniscus (Echiniscus) trisetosus from North America.

Schuster and Grigarick (1965) made the first report of this species in North America from collections which were made in California and Oregon.

The collection of this species from Montana constitutes the second record of Echiniscus (E.) trisetosus from North America.

Echiniscus (Echiniscus) trisetosus ecology notes.

Schuster and Grigarick (1965) reported twenty-five specimens from four samples: three of these were lichens, the fourth was not specified. The single example from Montana was found in the moss Rhytidiadephus triquetrus.

Genus Pseudechiniscus Thulin, 1911

> "Wie bei Echiniscus ist die Ruckenseite mit dinem Panzer bedeckt, der jedoch hier eine andere Zusammensetzung hat.
>
> I. Die Kopfplatte. - II. Die erste Rumpfplatte (die Schulterplatte). - III. Die erste Schaltplatte ist oft durch eine Querlinie zweigeteilt. Wenn sie eingach ist, grenzt sie immer unmittelbar an die Schulterplatte. - IV. Die zweite Rumpfplatte ist paarig. - V. Die zweite Schalplatte ist wie die erste oft doppelt und grenzt immer unmittelbar an die zweite Rumpfplatte. - VI. Die dritte Rumpfplatte, paarig, einen Halbrign bildend, bald durch eine mehr oder weniger deutliche, mediane, langsgehende Linie geteilt. - IX. Die Endplatte hat immer Kleeblattkerben aber keine Fazettierung.
>
> Der Bucallapparat stimmt mit dem bei Eichiniscus uberein. Die Mundhohle hat auch hier (wenigstens bei der Art, die ich zu untersuchen Gelegenheit gehabt habe) laterale Ausbuchtungen

> vor den Mundungen der Stilettscheiden. Die Mundrohre ist eng und gerade, die Stilette gerade ohne Stilettrager, der Schlundkopf relativ klein."

This genus resembles Echiniscus very closely because the dorsal surface is covered with four distinct plates. The taxonomic difference is that Pseudechiniscus has a pseudosegmental plate transverally situated between the terminal plate (E) and the dorsal plate (D).

As in Echiniscus, species determination is based on the number, length, and location of dorsal spines and lateral spines. Buccal cirri and sculptured texture or patterns on the plates are also often necessary for identification. Like Echiniscus, the four claws arise independently on each leg.

The lettering and numbering code for spines, plates and cirri are the same as those which were described for Echiniscus.

Two species of this genus were collected and identified from western Montana during this study.

Pseudechiniscus raneyi Grigarick, Mihelcic, and Schuster, 1964.

> "Length excluding legs IV about 300u, width 150u. Eyespots present, reddish. Cuticle of dorsal plates comprised of rather uniform polygons, somewhat larger toward the anterior margins of the dorsal and intersegmental areas and venter are smooth; venter without plates. Head and scapular plates appear subdivided by bands of smooth cuticle. Scapular, dorsal and pseudosegmental plates are to some extent longitudinally divided. Five lateral spines, moderately long at ends and shorter at middle of series; lateral spines measure 57u, 15u, 25u, 25u, and 175u. Long dorsal spines lacking but posterior edge of dorsal segments have numerous small spines of varying length. Head with internal cirrus short, 10u; papilla 9u long, almost as wide; external cirrus 25u. Leg I with small basal spine; leg IV with larger basal papilla. Internal claws of all legs recurved spur near base. Collar of leg IV with 8-10 teeth."

Pseudechiniscus raneyi from Montana.

Five specimens were collected in western Montana. Average length 182u, excluding legs IV, 80u to 215u. Eyespots present, dark. Polygonal pattern on cuticle of dorsal plates uniform and distinct. Spines present at A, B, C, D, and E. A and E greater in length than B, C, and D, which are nearly equal. Internal cirrus short; papilla broad and short. Internal claw with prominate recurved spur near base.

Pseudechiniscus raneyi from North America.

Described in 1964 by Grigarick, Mihelcic, and Schuster, Pseudechiniscus raneyi was found in the Sierra Nevada of California south of Lake Tahoe. At that time, Grigarick, et al, indicated a "definable distribution" for the four known species of Pseudechiniscus from North America. They stated that Pseudechiniscus suillus as reported by Mathews, (1938) was confined to Santa Cataline Island. Pseudechiniscus goedeni (Grigarick, Mihelcic, and Schuster, 1964) occurred in southwest Oregon. Pseudechiniscus victor was known only from northern California, whereas Pseudechiniscus raneyi was from the Sierra Nevada south of Lake Tahoe. Their conclusion, based on the data which had been collected, was "that no two species are present in any of these areas."

Schuster and Grigarick (1965) expanded the known range of Pseudechiniscus raneyi into northern California and Oregon. The ranges of Psdudechiniscus goedeni, and Pseudechiniscus victor were not expanded. The question of "definable distributions" and "two species present in any one area," was not mentioned.

The collection in Montana of both Pseudechiniscus raneyi and Pseudechiniscus victor further extends the known ranges in North America for both species. The removal of both species from the same moss at site 23B is the first reported occurrence of two species of Pseudechiniscus not only in the same area but in the same species of plant. The identification of the individuals involved were confirmed by Robert O. Schuster, University of California at Davis.

In their 1965 paper, Schuster and Grigarick, stated that Pseudechiniscus raneyi in the southern part of its range, has spines at B, C, and D. (plate 1, fig. A.) of approximately equal length, smaller than either spines A or E. In the northern areas of California and Oregon the specimens showed spine C as being longer than B and D but not as long as A or E. The examples from Montana do not have the spine pattern like those of northern California. They are similar to the southern California types with spines B, C, and D about equal in length, C is not elongated.

Pseudechiniscus raneyi ecology notes.

Of the nine collections in California and Oregon, seven were from lichens, one was from a moss and the last was not distinguished. In six of these collections the substrate was a tree, most often Pinus or Abies. Plant identification was not reported.

Two of the three samples from Montana were mosses, although in each case only a single tardigrade was found. The third sample was a lichen from which three specimens were removed, but like the two mosses, the lichen was on a soil substrate, not a tree as reported in the work in California.

Because of the relatively few numbers of Pseudechiniscus raneyi found to date, no conclusions can be drawn. However, it does occur in western Montana, and it has been found in plants with a soil base as the twenty-two samples of mosses and lichens from trees did not yield any examples of this species.

Pseudechiniscus victor (Ehrenberg, 1853)

The original description is not available.

Pseudechiniscus victor from Montana.

Four specimens of Pseudechiniscus victor were collected from western Montana. Average length 188u, excluding legs IV, range of measurements from 135u to 236u. Eyespots present. Dorsal plate sculpture appearing regular, patterned, polygonal. Claws with basal spur. Lateral spines present at A, B, C, D, and E. Laterla spines A and E long. Lateral spines B, C, and D short, stout. Dorsal spines on C and D. Collar on legs IV with large teeth, few in number. Buccal cirri bifurcate.

Pseudechiniscus victor from North America.

Pseudechiniscus victor was first reported from North America by Grigarick, Mihelcic, and Schuster (1964) from northern California. Schuster and Grigarick (1965) reported this speices from California and Oregon.

This report constitutes the third reported occurrence of Pseudechiniscus victor in North America.

Schuster and Grigarick (1965) reported ninety-five specimens from three sites.

Four specimens of Pseudechiniscus victor were collected in western Montana.

Pseudechiniscus victor ecology notes.

Schuster and Grigarick (1965) reported both mosses and lichens as the habitats for this species.

The examples of Pseudechiniscus victor from Montana all came from the same moss Dicranum bonjeanil. Pseudechiniscus raneyi was found in the same moss sample as Pseudechiniscus victor. (See Pseudechiniscus raneyi for discussion).

CHAPTER VI

MATHEMATICAL MEASURES OF ASSOCIATION AMONG SPECIES OF TARDIGRADES

Two standard statistical tests, chi-square and Cole's coefficient, were applied to the data to determine if interspecific associations existed between the species of tardigrades found.

Species which occurred in less than 6% of the samples were considered too scarce for associational determinations. For this reason, species which did not occur in a least four samples were excluded.

Table #1 presents joint occurrence data. The observed number of joint occurrences in most cases is not significantly different from the expected number of joint occurrences.

The half of Table #2 presents chi-square data. Chi-square (Siegel, 1956) measures departure from a random pattern of co-occurrence. The resultant numbers must be greater than 3.84 in order to be significant values of chi-square and to demonstrate a confidence level of P 0.05 with one degree of freedom.

A majority of the chi-squares in Table #2 are below 1.00 and none of the chi-squares in Table #2 are greater than 3.84. The bottom half of Table #2 presents Cole's Coefficient data. Cole's Coefficient (Cole, 1949) measures interspecific association and expresses that association

TABLE 1

EXPECTED AND OBSERVED JOINT OCCURANCE[1] OF SELECTED SPECIES OF TARDIGRADA FROM WESTERN MONTANA

	# of Samples	M. harmsworthi	M. hufelandii	M. richtersi	H. alpinus	H. oculatus	H. scoticus	H. convergens	H. oberheauseri
M. harmsworthi	28		21.0	13.0	3.0	4.0	4.0	10.0	6.0
M. hufelandii	41	21.6		12.0	4.0	2.0	4.0	12.0	8.0
M. richtersi	17	9.3	13.1		2.0	2.0	1.0	6.0	2.0
H. alpinus	4	2.1	3.1	1.3		0.0	0.0	1.0	0.0
H. oculatus	4	2.1	3.1	1.3	0.30		0.0	2.0	2.0
H. scoticus	5	2.6	3.9	1.6	0.38	0.38		2.0	1.0
H. convergens	14	7.4	10.8	4.5	1.0	1.0	1.3		6.0
H. oberheauseri	11	5.8	8.6	3.5	0.83	0.83	1.0	2.9	

Observed - above diagonal

Expected - below diagonal

TABLE 2

COLE'S COEFFICIENT[1] AND CHI-SQUARE[2] FOR SELECTED SPECIES OF TARDIGRADA FROM WESTERN MONTANA

	# of Samples	M. harmsworthi	M. hufelandii	M. richtersi	H. alpinus	H. oculatus	H. scoticus	H. convergens	H. oberheauseri
M. harmsworthi	28		0.01	1.40	0.40	1.70	0.50	0.91	0.07
M. hufelandii	41	-.14		1.19	0.20	0.30	0.30	0.01	0.004
M. richtersi	17	0.50	-.14		0.30	0.30	0.20	0.50	0.60
H. alpinus	4	0.47	1.00	0.26		0.30	0.40	0.00	0.80
H. oculatus	4	1.00	0.30	0.26	-1.0		0.40	1.00	1.80
H. scoticus	5	0.57	1.00	0.37	-1.0	-1.0		0.10	0.00
H. convergens	14	0.39	-.09	0.17	-.05	0.32	0.19		3.30
H. obereauseri	11	0.22	-.30	-.45	-1.0	0.37	-.40	0.33	

1. below diagonal
2. above diagonal

as a number between -1 and +1. The majority of Cole's Coefficients in Table #2 do not approach a significant level.

Four of the combinations do indicate a total negative association with -1. In each case these are rare species in association with other. The chi-square determinations are all below 1.00, which indicates that this is probably a totally random lack of association. The expected joint occurrences of these associations are less than 1.00. For these reasons a Cole's Coefficient of -1 is not significant in Table #2.

Two of the combinations do indicate a total positive association with +1. In both cases a very abundant species occurred in every collection of a less abundant species. The chi-square determinations of 1.70 and 0.20 indicate that these are most likely random associations. The differences between observed and expected joint occurrences are not large enough to suggest anything except a random occurrence of each species. For these reasons a Cole's Coefficient of +1 is not significant in Table #2.

CHAPTER VII

SUMMARY

The Phylum Tardigrada is a cosmopolitan group of animals which had not previously been reported from Montana. During the course of this investigation, over one thousand specimens of tardigrades from western Montana were studied. Five genera and twenty species are reported. One of these species is reported for the first time from North America. This report also constitutes the second report from North America for three other species, and the third report of an additional five species from this continent.

A key has been constructed to the species which were found in western Montana. The key is based on morphological structures which are easily visible on properly mounted specimens.

Some of the problems in the ecology of the Tardigrada of North America have been presented. This work contributes not only to the world distributional patterns of these animals but presents ecological associations which until now have been unreported.

This work should point the direction to further investigation into other animals that live in the same micro-environment.

APPENDIX A

DISTRIBUTIONAL DATA FOR TARDIGRADA FROM WESTERN MONTANA

Because no previous records exist for the phylum Tardigrada from western Montana, these records constitute valid range extentions for each species which is discussed.

For the collection data which follows, all specimens in this paper were collected by the author and are in his personal collection. A sample of most species mentioned in this study will be donated to the University of Montana Invertebrate Museum.

These data are arranged by species, following the arrangement in the text. Localities are listed under each species by county and the counties are listed South to North.

The code numbers listed with each site are first: the author's collection number; second: plant identification number; and third: slide numbers in which these specimens are mounted.

Macrobiotus areolatus Murray, 1907

Lake County

McDonald cirque, Mission mountains, T.19N., R.18W., Sec.17, June 25, 1967, (2C; 31, 17; 62)

Mission mountains, McDonald cirque, Round lake, T.19N., R.18W., Sec.5, June 25, 1967, (3A; ---; 75)

University of Montana Biological Station, Flathead lake, T.24N., R.19W., Sec.4, June 22, 1967, (1B; 53; 25)

Macrobiotus harmsworthi Murray, 1907

Granite County

Junction of Skalkaho pass and Rock Creek roads. T.6N., R.16W., Sec. 31, July 2, 1967, (22A; lichen; 94, 95), (22B; 50; 49, 52, 96, 98, 99, 100)

Rock Creek road, Bitterroot flats, T.8N., R.17W., Sec.7, July 2, 1967, (23B; 7; 102, 106, 107)

Ravalli County

Sula, East fork of the Bitterroot. T.1N., R.19W., Sec.22, July 1, 1967. (17A; 35; 78, 79)

Jim Hell Rock, East Fork of the Bitterroot. T.2N., R.19W., Sec.7, July 1, 1967. (18A; 4; 8), (18B; lichen; 10)

Top Skalkaho pass, Sapphire mountains. T.6N., R17W., Sec.29. July 1, 1967. (20A; 3; 89, 92)

Missoula County

Holland lake, Swan Valley. T.16N., R.20W., Sec.33. July 22, 1967. (85B; 35; 232, 234)

Sanders County

Bull lake. T.57N., R.33W., Sec.34. July 15, 1967. (54A; lichen; 181), (54B; 28; 185)

Bull River Campground. T.54N., R.33W., Sec.10. July 15, 1967. (55A; 11; 189)

Lake County

University of Montana Biological Station, Flathead Lake. T.24N., R.19W., Sec.4. June 22, 1967. (1B; 53; 27, 28)

McDonald cirque, Mission mountains. T.19N., R.18W., Sec.17. June 25, 1967. (2C; 31, 17; 62, 63, 66, 68)

Wolf Creek, Swan Valley. T.27N., R.19W., Sec.23. July 10, 1967. (47A; lichen; 156, 158, 160, 161, 162), (47D; 5; 165)

Rippling Waters Bridge, Swan Valley. T.26N., R.19W., Sec. 11. July 10, 1967. (49A; 35; 56-59, 166-170)

Big Arm, Flathead Lake. T.24N., R.21W., Sec. 16. July 15, 1967. (58A; 35; 195-198)

Flathead County

McWininger slough, Kalispell. T.28N., R.21W., Sec.1. July 3, 1967. (24A; 41; 111)

Hell Roaring Creek, North Fork of the Flathead river. T.32N., R.20W., Sec.3. July 7, 1967. (28C; --; 123-125, 127)

Top of Trail Creek pass, Whitefish mountains. T.37N., R.24W., Sec.33. July 7, 1967. (35A; --; 130)

Dicky Lake, Stillwater Valley. T.34N., R.25W., Sec.11. July 7, 1967. (38A; 36; 145-147)

McGregor Lake, west of Kalispell. T.26N., R.26W., Sec.1. July 15, 1967. (50A; 19; 171), (50B; lichen; 174,175)

Lincoln County

Graves Creek, Stillwater Valley. T.35N., R.19W., Sec.14. July 7, 1967. (36A; 48; 134-136, 139-141)

Glacier National Park

South of McDonald Lake, G.N.P. T.32N., R.18., Sec.5. July 8, 1967. (40B; 56; 148-153)

McGee's Meadow, G.N.P. T.33N., R.19W., Sec.22. July 17, 1967. (50C; lichen; 201)

Camas Creek, G.N.P. T.33N., R.19W., Sec.14. July 17, 1967. (62A; 28; 213-216)

Logging Creek, G.N.P. T.34N., R.20W., Sec.16. July 17, 1967. (62A; 28; 213-216)

Macrobiotus hufelandii Schultz, 1834

Granite County

Junction of Skalkaho pass and Rock creek roads. T.6N., R.16W., Sec.31. July 2, 1967. (22A; lichen; 95), (22B; 7; 49, 50, 96, 97, 101)

Rock Creek road, Bitterroot Flats. T.8N., R.17W., Sec.7, July 2, 1967. (23B; 7; 105, 109)

Ravalli County

Sula, East Fork of the Bitterroot. T.1N., R.19W., Sec.22. July 1, 1967. (17A; 35; 76-79)

Jim Hell Rock, East Fork of the Bitterroot. T.2N., R.19W., Sec.7. July 1, 1967. (18A; 4; 8, 9), (18B; lichen; 10)

Skalkaho pass, Sapphire Mountains. T.5N., R.18W., Sec. 18. July 1, 1967. (19A; 28; 11, 12), (19B; 12; 13-16)

Top Skalkaho pass, Sapphire Mountains. T.6N., R.17W., Sec.29. July 1, 1967. (20A; 3; 89-92)

Bass Creek, Bitterroot Mountains. T.10N., R.20W., Sec.32. July 1, 1967. (12B; lichen; 80)

Powell County

McDonald pass, Highway U.S. 12. T.9N., R.6W., Sec.1. July 22, 1967. (79B; 32; 225-227)

Missoula County

Seely Lake, Clearwater Valley. T.17N., R.15W., Sec.17. July 22, 1967. (84A; 4; 229, 231)

Holland Lake, Swan Valley. T.16N., R.20W., Sec.33. July 22, 1967. (85B; 35; 232-239)

Sanders County

Bull Lake. T.57N., R.33W., Sec.34. July 15, 1967. (54B; 28; 182-186)

Bull River Campground. T.54N., R.33W., Sec.10. July 15, 1967. (55A; 11; 188-190)

Rainbow Lake. T.25N., R.20W., Sec.3. July 15, 1967. (57A; 4; 191, 192)

Highway 20, between Perma and Dixon. T.18N., R.22W., Sec.19. July 20, 1967. (68A; 35; 224)

Lake County

University of Montana Biological Station, Flathead Lake. T.24N., R.19W., Sec.4. June 22, 1967. (1D; --; 24)

McDonald Cirque, Mission Mountains. T.19N., R.18W., Sec.17. June 25, 1967. (2C; 31; 17; 61-70), (2A; 58; 72)

Between Frog & Summit Lakes, Mission Mountains. T.19N., R.18W., Sec.5. June 25, 1967. (4C; 61; 35-43), (4D; lichen; 32-34)

Round Lake, Mission Mountains. T.19N., R.18W., Sec.5. June 25, 1967. (3A; --; 74, 75)

Wolf Creek, Swan Valley. T.27N., R.19W., Sec.23. July 10, 1967. (47D; 5; 159, 163)

Rippling Waters Bridge, Swan Valley. T.26N., R.19W., Sec.11. July 10, 1967. (49A; 35; 56-59, 166-170)

Big Arm, Flathead Lake. T.24N., R.21W., Sec.16. July 15, 1967. (58A; 35; 195-198)

Flathead County

Whitefish Lake. T.31N., R.22W., Sec.4. June 29, 1967. (11B; 7; 83-85)

McWininger slough, Kalispell. T.28N., R.21W., Sec.1. July 3, 1967. (24A; 41; 110)

Hell Roaring Creek, North Fork of the Flathead river. T.32N., R.20W., Sec.3. July 7, 1967. (28B; 46; 114-120)

Trail Creek, North Fork of the Flathead river. T.37N., R.23W., Sec.27. July 7, 1967. (30A; fungi; 235, 236)

McGregor Lake, west of Kalispell. T.26N., R.26W., Sec.1. July 15, 1967. (50A; 19; 172), (50B; lichen; 173-179)

Glacier National Park

South of Lake McDonald. G.N.P. T.32N., R.18W., Sec.14. July 8, 1967. (40B; 56; 148-153)

McGee's Meadow. G.N.P. T.33N., R.19W., Sec.14. July 17, 1967. (60B; 43; 199), (60D; 9, 12; 202-207)

Camas Creek. G.N.P. T.33N., R.19W., Sec.14. July 17, 1967. (61A; 1; 208), (61B; 22, 49; 212), (61C; --; 17-23, 209-211)

Logging Creek. G.N.P. T.34N., R.20W., Sec.16. July 17, 1967. (62A; 28; 215)

Quartz Creek. G.N.P. T.34N., R.20W., Sec.7. July 17,1967. (63A; 47; 217-220)

<u>Macrobiotus islandicus</u> Richters, 1903

Ravalli County

Skalkaho pass, Sapphire Mountains. T.5N., R.18W., Sec.18. July 1, 1967. (19B; 12; 13)

Flathead County

McWininger slough, Kalispell. T.28N., R.21W., Sec.1. July 3, 1967. (24A; 41; 111)

Macrobiotus richtersi Murray, 1911

Missoula County

Holland Lake, Swan Valley. T.16N., R.20W., Sec.33. July 22, 1967. (85B; 35; 232)

Seely Lake, Clearwater Valley. T.17N., R.15W., Sec.17. July 22, 1967. (84A; 4; 228-230)

Sanders County

Bull Lake. T.57N., R.33W., Sec.34. July 15, 1967. (54B; 28; 183, 185), (54A; lichen; 180)

Lake County

University of Montana Biological Station, Flathead Lake. T.24N., R.19W., Sec.4. June 22, 1967. (1B; 53; 27-29)

McDonald cirque, Mission Mountains. T.19N., R.18W., Sec.17. June 25, 1967. (2C; 31, 17; 61, 64, 67, 68)

Wolf Creek, Swan Valley. T.27N., R.19W., Sec.23. July 10, 1967. (47D; 5; 164)

Rippling Waters Bridge, Swan River. T.26N., R.19W., Sec.11. July 10, 1967. (49A; 35; 58)

Big Arm, Flathead Lake. T.24N., R.21W., Sec.16. July 15, 1967. (58A; 35; 60, 197)

Flathead County

McWininger slough, Kalispell. T.28N., R.21W., Sec.1. July 3, 1967. (24A; 41; 110)

Hell Roaring Creek, North Fork of the Flathead River. T.32N., R.20W., Sec.3. July 7, 1967. (28B; 46; 122)

Top of Trail Creek pass, Whitefish Mountains. T.37N., R.24W., Sec.33. July 7, 1967. (35A; --; 128, 129)

Lincoln County

Graves Creek, Stillwater River. T.35N., R.26W., Sec.14. July 7, 1967. (36A; 48; 133, 135, 136, 139-144)

Dicky Lake, Stillwater Valley. T.34N., R.25W., Sec.11. July 7, 1967. (38A; 36; 145, 146)

Glacier National Park

Logging Creek, G.N.P. T.34N., R.20W., Sec.16. July 17, 1967. (62A; 28; 213-216)

Quartz Creek. G.N.P. T.34N., R.20W., Sec.7. July 17, 1967. (63A; 47; 217-220), (63B; 19; 221)

Hypsibius (D) alpinus (Murray, 1906)

Lake County

Between Frog & Summit Lakes, Mission Mountains. T.19N., R.18W., Sec.5. June 25, 1967. (4C; 61; 40)

Flathead County

McWininger slough, Kalispell. T.28N., R.21W., Sec.1. July 3, 1967. (24A; 41; 111)

Glacier National Park

South of Lake McDonald. T.32N., R.18W., Sec.5. July 8, 1967. (40B; 56; 153)

Camas Creek. G.N.P. T.33N., R.19W., Sec.14. July 17, 1967. (61C; --; 211)

Hypsibius (D) angustatus (Murray, 1905)

Ravalli County

Top of Skalkaho pass, Sapphire Mountains. T.6N., R.17W., Sec.29. July 1, 1967. (20B; 37; 93)

Hypsibius (D) arduifrons (Thulin, 1928)

Granite County

Junction of Skalkaho pass and Rock Creek Roads. T.6N., R.16W., Sec.31. July 2, 1967. (22B; 50; 46, 47, 50, 96, 98, 99, 101)

Rock Creek road, Bitterroot flat. T.8N., R.17W., Sec.7. July 2, 1967. (23B; 7; 102, 106)

Hypsibius (D.) oculatus (Murray, 1906)

Granite County

Rock Creek road, Bitterroot flat. T.8N., R.17W., Sec.7. July 2, 1967. (23B; 7; 102, 105)

Lake County

University of Montana Biological Station, Flathead Lake. T.24N., R.19W., Sec.4. June 22, 1967. (1B; 53; 27)

Lincoln County

Graves Creek, Stillwater Valley. T.35N., R.26W., Sec.14. July 7, 1967. (36A; 48; 140)

Flathead County

Hell Roaring Creek, North Fork of the Flathead river. T.32N., R.20W., Sec.3. July 7, 1967. (28C; --; 124)

Hypsibius (D.) scoticus (Murray, 1905)

Ravalli County

Top of Skalkaho pass, Sapphire Mountains. T.6N., R.17W., Sec.29. July 1, 1967. (20A; 3; 89)

Sanders County

Bull Lake. T.57N., R.33W., Sec.34. July 15, 1967. (54B; 28; 182-186)

Bull River Campground. T.54N., R.33W., Sec.10. July 15, 1967. (55A; 11; 189)

Flathead County

McGregor Lake, west of Kalispell. T.26N., R.26W., Sec.1. July 15, 1967. (50A; 19; 171)

Glacier National Park

McGee's meadow, G.N.P. T.33N., R.19W., Sec.22. July 17, 1967. (60B; 43; 199)

Hypsibius (D.) spitzbergensis (Richters, 1903)

Ravalli County

Skalkaho pass, Sapphire Mountains. T.5N., R.18W., Sec.18. July 1, 1967. (19A; 28; 11)

Sanders County

Bull River Campground. T.54N., R33W., Sec.10. July 15, 1967. (55A; 11; 189)

Lake County

McDonald Cirque, Mission Mountains. T.19N., R.18W., Sec.5. June 25, 1967. (3A; --; 73)

Hypsibius (H.) convergens (Urbanowicz, 1925)

Granite County

Junction of Skalkaho pass and Rock Creek roads. T.6N., R.16W., Sec.31. July 2, 1967. (22A; lichen; 94), (22B; 30; 46, 47, 97-100, 113)

Rock Creek Road, Bitterroot flat. T.8N., R.17W., Sec.7. July 2, 1967. (23B; 7; 102, 105, 106, 108)

Missoula County

Highway between Perma & Dixon. T.18N., R.22W., Sec.19. July 20, 1967. (68A; 35; 224)

Sanders County

Bull Lake. T.57N., R.33W., Sec.34. July 15, 1967. (54A; lichen; 185)

Lake County

University of Montana Biological Station, Flathead Lake. T.24N., R.19W., Sec.4. June 22, 1967. (1B; 53; 27-29)

Round Lake, Mission Mountains. T.19N., R.18W., Sec.5. June 25, 1967. (3A; --; 75)

Wolf Creek, Swan Valley. T.27N., R.19W., Sec.23. July 10, 1967. (47D; 5; 165)

Flathead County

McWininger slough, Kalispell. T.28N., R.21W., Sec.1. July 3, 1967. (24A; 41; 111)

McGregor Lake, west of Kalispell. T. 26N., R.26W., Sec.1. July 15, 1967. (50A; 19; 172)

Top of Trail Creek pass, Whitefish range. T.37N., R.24W., Sec.33. July 7, 1967. (35A; --; 131)

Glacier National Park

McGee's Meadow, G.N.P. T.33N., R.19W., Sec.22. July 17, 1967. (50C; lichen; 201)

Camas Creek. T.33N., R.19W., Sec.14. July 17, 1967. (61A; 1; 208)

Quartz Creek. T.34N., R.20W., Sec.7. July 17, 1967. (63A; 47; 220)

Hypsibius (H.) oberhaeuseri (Doyere, 1840)

Granite County

Junction of Skalkaho pass and Rock Creek Roads. T.6N., R.16W., Sec.31. July 2, 1967. (22B; 50; 44), (22A; lichen; 94)

Rock Creek Road, Bitterroot flats. T.8N., R.17W., Sec.7. July 2, 1967. (23B; 7; 102, 105, 109)

Ravalli County

Bass Creek, Bitterroot mountains. T.10N., R.20W., Sec.32. July 1, 1967. (12B; lichen; 80, 81)

Skalkaho pass, Sapphire mountains. T.5N., R.18W., Sec.18. July 1, 1967. (19C; lichen; 86, 87, 88)

Lake County

University of Montana Biological Station, Flathead Lake. T.24N., R.19W., Sec.4. June 22, 1967. (1B; 53; 27-29)

Between Frog & Summit Lakes, Mission Mountains. T.19N., R.18W., Sec.5. June 25, 1967. (4A; --; 71)

Powell County

Top of McDonald pass, Highway 12. T.9N., R.6W., Sec.1. July 22, 1967. (79B; 32; 226)

Flathead County

Whitefish Lake. T.31N., R.22W., Sec.4. July 29, 1967. (11B; 7; 84, 85)

Top of Trail Creek pass, Whitefish range. T.37N., R.24W., Sec.33. July 7, 1967. (35A; --; 131)

McGregor Lake, west of Kalispell. T.26N., R.26W., Sec.1. July 15, 1967. (50A; 19; 172)

Milnesium tardigradum Doyere, 1840

Sanders County

Bull River Campground. T.54N., R.33W., Sec.10. July 15, 1967. (55A; 11; 187, 190)

Rainbow Lake. T.25N., R.20W., Sec.3. July 15, 1967. (57A; 4; 194)

Lake County

Big Arm, Flathead Lake. T.24N., R.21W., Sec.16. July 15, 1967. (58A; 35; 196, 198)

Hypsibius (I.) prosostomus (Thulin, 1928)

Flathead County

Hell Roaring Creek, North Fork of the Flathead River. T.32N., R.20W., Sec.3. July 7, 1967. (23C; --; 124)

Echiniscus (E.) arctomys Ehrenberg, 1853

Lake County

McDonald cirque, Mission Mountains. T.19N., R.18W., Sec.17. June 25, 1967. (2C; 31, 17; 62)

Echiniscus (E.) quadrispinosus Richtersi, 1902

Ravalli County

Skalkaho pass, Sapphire mountains. T.5N., R.18W., Sec.18. July 1, 1967. (19A; 28; 11)

Flathead County

Whitefish Lake. T.31N., R.22S., Sec.4. June 29, 1967. (11B; 7; 83-85)

Echiniscus (E.) trisetosus Cuenot, 1932

Lake County

McDonald cirque, Mission Mountains. T.19N., R.18W., Sec.17, June 25, 1967. (2C; 31, 17; 62)

Pseudechiniscus raneyi Grigarick, Mihelcic, & Schuster 1964

Granite County

Rock Creek Road, Bitterroot Flat. T.8N., R.17W., Sec.7. July 2, 1967. (23B; 7; 103)

Flathead County

McWininger slough, Kalispell. T.28N., R.21W., Sec.1. July 3, 1967. (24A; 41; 110)

McGregor Lake, west of Kalispell. T.26N., R.26W., Sec.1. July 15, 1967. (50B; lichen; 177)

Pseudenchiniscus victor (Ehrenberg, 1853)

Granite County

Rock Creek, Bitterroot Flat. T.8N., R.17W., Sec.7. July 2, 1967. (23B; 7; 102, 104, 109)

APPENDIX B

HABITAT

During this study, an effort was made to define the habitat in which tardigrades were found. The present assemblage of literature contributes little knowledge of the ecology of the tardigrada.

Higgins (1959) reported finding tardigrades in only three species of mosses. These are discussed in the text. Puglia (1959) reported habitats only as: moss, lichen, forest litter, or aquatic. Riggin (1962) gave excellent descriptions of the animals, and good collection data, but did not indicate the habitat from which the specimens were removed. Riggin (1964) followed the same pattern of not reporting habitat data.

Schuster and Grigarick (1965) reported both habitat and a substrate wherever possible.

This work contributes not only a large number of moss habitats identified to species but includes data which suggest a lack of interspecific relationships among species of the Tardigrada.

Large scale comparison of this information is impossible because of the incomplete nature of previous reports of habitat and substrate.

Fantaham and Porter (1945) worked with the protozoan fauna of the mosses of central Canada. They identified mosses and protozoa

and listed other animals such as "tardigrades" as present. They state:

> "Tardigrada were always in small numbers and patchy in distribution. Being bryophagous they could not live among the mosses with tougher leaves, for which their minute teeth were quite unadapted....Tardigrada and Gastrotricha were found in the softer mosses only. Macrobiotus and Echiniscus were the principle tardigrades in our collection; species of Diphascon and Milnesium were rare."

The comparison of the data of Fantaham and Porter (1945) with that from Montana presents some interesting contridictions.

Four samples of mosses of the genus Polytrichum which were collected in Canada yielded tardigrades whereas the collection of five samples of the same genus of moss in Montana was without tardigrades.

In the work from Canada, one sample out of seven of the mosses of the genus Brachythecium sp. yielded tardigrades, whereas eight out of ten samples of this same genus of moss from Montana contained tardigrades.

Data of this nature raise the questions of why an animal with what seems to be quite broad requirements for suitable habitats is found in one sample and not in another.

Schuster and Grigarick (1965) said, "We have not seen a single paper delimiting the precise conditions under which a species goes about living normally."

This study does not advance any theories on the associations between tardigrades and habitats, but does contribute data so that some day the "precise conditions under which a species goes about living normally" may be construed.

APPENDIX C

LIST OF SPECIES OF TARDIGRADA FROM NORTH AMERICA

Species	Reference[1]
Batillipes friaufi	8
" mirus	4
" pennaki	4
Bathyechiniscus tetronyx	2
Echiniscoides sigismundi	7, 9
Echiniscus (E.) arctomy	8, 9, X
" " blumi	8, 9
" " bisetosus	6, 8
" " canadensis	5, 6
" (H.) gladiator	6, 8, 9
" (E.) granulatus	8
" (B.) intermedius	6, 1
" (E.) mauccii	8
" " merokensis	5, 8
" " multispinosus	9
" " oihonnae	6, 8, 9
" " phacae	8
" " quadrispinosus	9, X
" (B.) parvulus	5
" (E.) reymondi	5
" " robertsi	9
" " sylvanus	6
" " testudo	9
" " trisetosus	9, X
" " virginicus	8
" " wendti	8, 9
Haplomacrobiotus hermosillensis	9
Hypsibius (D.) ordatus	9
" " alpinus	6, 9, X
" " angustatus	8, 9, X
" " arduifrons	X, New, N. America
" " belgicae	8, 9
" " bullatum	8
" " chilenensis	6
" " nodulosus	8, 9
" " oculatus	7, 9, X
" " pinguis	8
" " iltisi	9

Species	Reference
Hypsibius (D.) scoticus	6, 8, 9, X
" " spitzbergensis	9, X
" " stappersi	9
" (H.) articus	6
" " calcaratus	9
" " conjungens	8
" " convergens	8, 9, X
" " dujardini	8
" " oberhaeuseri	5, 6, 9, X
" " pallidus	8
" (I.) augusti	4, 9
" " canadensis	5, 6, 8
" " granulifer	8
" " nodosus	8
" " prosostomus	8, 9, X
" " sattleri	6, 9
" " tetradactyloides	8
" " schaudinni	8
" " tuberculatus	6, 8, 9
Itaquascon umbellinae	8
Macrobiotus areolatus	6, 9, X
" echinogenitus	6, 8
" furcatus	7
" harmsworthi	8, 9, X
" hufelandii	6, 8, 9, X
" intermedius	8
" islandicus	8, 9, X
" macronyx	8, 9
" ovovillosus	1
" richtersi	8, 9, X
" tonollii	8
" occidentalis	6
" virgatus	6
Milnesium tardigradum	8, 9, X
Pseudechiniscus goedeni	3, 9
" novaezeelandiae	7
" ramazzotti	8
" raneyi	3, 9, X
" suillus	5, 8, 9
" victor	3, 9, X
Styraconyx sargassi	7, 9

Modified from Schuster and Grigarick, 1965

1. Baumann, 1969
2. Chitwood, 1954
3. Grigarick, et al., 1964
4. Higgins, 1959

5. Mathews, 1938
6. Murray, 1910
7. Ramazzotti, 1962
8. Riggins, 1962
9. Schuster & Grigarick, 1965
X. Present study

[1]References are listed in the Bibliography.

APPENDIX D

NEGATIVE DATA

The following is a list of plants which yielded no tardigrades, along with the conditions under which each was collected. The collection site and number of samples of this species of plant is also included.

This is not intended to indicate that tardigrades do not live in these plants, but that in the plant, at that time and under those conditions, no tardigrades were found. In fact, there are several occasions when tardigrades were present in one sample and were absent in another sample of the same species of plant habitat.

1. Drepanocladus aducus (Hedw.) Warnst. (5)
   - 22C Moist on the ground — Junc. Skalkaho Pass, Rock Cr. Granite Co.
   - 25A Moist on a rock — Daphina pond, Flathead Co.

2. Drepenocladus exannulatus (Guemb) Warnst. (1)
   - 7A Dry on snow — Eagle Pass, Missions, Lake Co.

4. Brachythecium alicans (Hedw.) Bry. Eur. (4)
   - 70B Dry on the ground — St. Regis, Hwy 10, Mineral Co.

5. Brachythecium lamprochryseum C. M. 7 Kinb. (2)
   - 53A Moist on a rock — Libby, Hwy 2, Lincoln

10. Dicranum scoparium Hedw. (1)
    - 65B Dry on the ground — St. Marys Lake, Lake Co.

11. Dicranum tauricum (4)
    - 23A Dry on the ground — Rock Cr., Granite Co.

13. Pohlia cruda (Hedw.) Lindb. (1)
    8A Moist on a rock — Hungry Horse Dam, Flathead Co.

14. Pohlia wahlenbergii (W. & M.) Andr. (1)
    28A Moist on the ground — Hell Roaring Cr., Flathead Co.

15. Barbula fallax Hedw. (2)
    8A Same as #13 above

19. Polytrichum juniperinum Hedw. (4)
    22C Moist on the ground — Rock Cr. Rd., Granite Co.

20. Polytrichum piliferum Hedw. (1)
    30B Dry ground — 2 Mi. Trail Cr., Flathead Co.

21. Bryum Sp. (4)
    42B Moist on the ground — Going to Sun Hwy, GNP
    46A Moist on the ground — Mud Cr., Flathead Co.

23. Campylium stellatum (Hedw.) L. 7 Jens. (1)
    51A Moist on the ground — Lower Thompson Lk., Sanders Co.

24. Campylium rapicale (1)
    24B Moist on the ground — McWinninger slough, Flathead Co.

26. Aulacomnium palustre Schw. (2)
    21B Moist on the ground — Skalkaho Pass, Granite Co.
    42A Moist on a rock — Going to Sun Hwy, GNP

27. Funaria hygrometrica Hedw. (1)
    76A Dry ground — Deerlodge Co.

33. Ceratodon purpureus (Hedw.) Brid. (4)
    21A Dry on the ground — Skalkaho Pass, Granite Co.
    83A Moist on the ground — Harper Lake, Missoula Co.

35. Homalothecium nevadense (Lesq.) R. & C. (8)
    56A Dry on the rock — Thompson River, Sanders Co.

38. Philonotis fontana (Hedw.) Bird (4)
    21C Moist on the ground — Skalkaho Pass, Granite Co.
    34A Moist on a rock — Top Trail Cr., Flathead Co.
    42B Moist on the ground — Going to Sun Hwy, GNP
    46A Moist on the ground — Mud Cr., Flathead Co.

39. Pottia hemi (Hedw.) Fuern (1)
    83A Moist on the ground — Harpers Lk., Missoula Co.

40. Tortula ruralis (Hedw.) Smith. (3)
    22C Moist on the ground — Rock Cr. Rd., Granite Co.

41. Leptodictyum riparium (Hedw.) Warnst. (2)
    84D Aquatic — Seeley Lake, Missoula Co.

43. Sphagnum Sp. (2)
    60A Wet bog — McGee's Meadow, GNP

48. Cratoneuron filicinium (Hedw.) Roth
    8B Moist on a rock — Hungry Horse Dam, Flathead Co.
    10A Moist on a rock — Berne Rest Area, Flathead Co.

51. Calliergon cordifolium (Hedw.) Kindb.
    21B Moist on the ground — Skalkaho Pass, Granite Co.
    37A Aquatic — Graves Cr., Lincoln Co.

57. Brachythecium rivulare Bry. Eur. (1)
    47B Moist on a log — Wolf Cr., Flathead Co.

67. Pseudoleskea radicosa (Mitt.) L. & J.
    43B Dry on a rock — Top Logan Pass, GNP

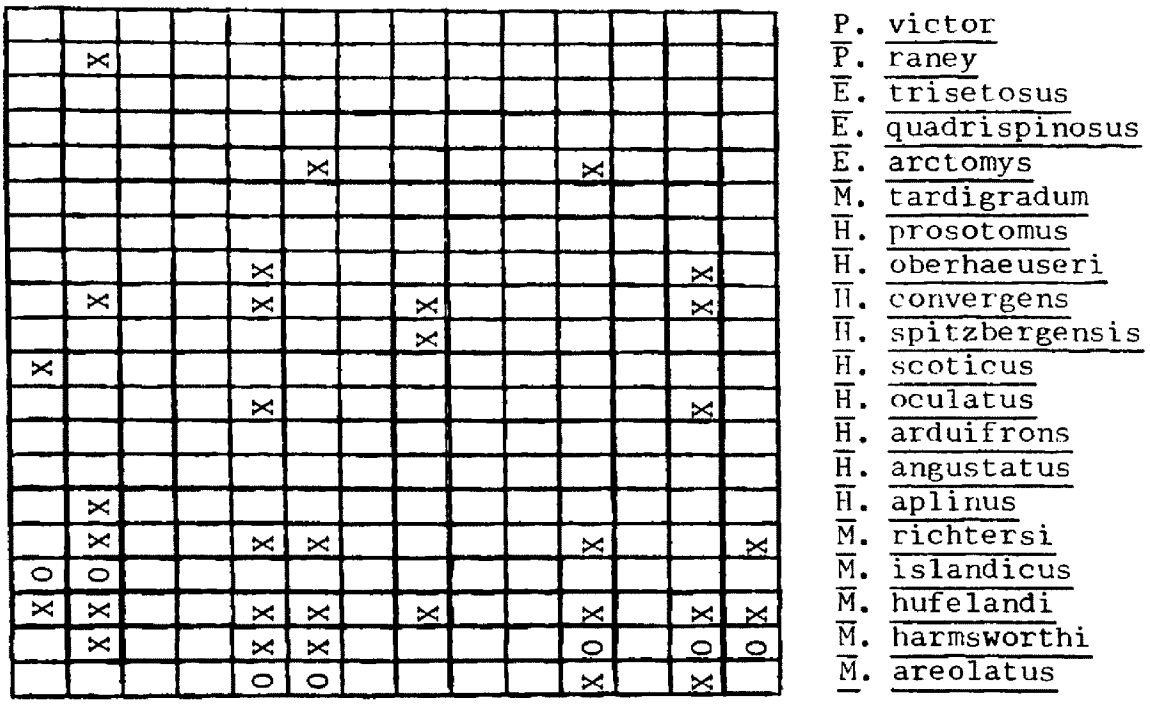
68. Fontinalis hypnordes (1)
    49B Aquatic — Rippling Waters, Flathead Co.

APPENDIX E

ECOLOGICAL DATA

Ecological data for the members of the several genera are arranged to illustrate the associational patterns, both positive and negative, between the species.

Ecological Data for the Genus Macrobiotus

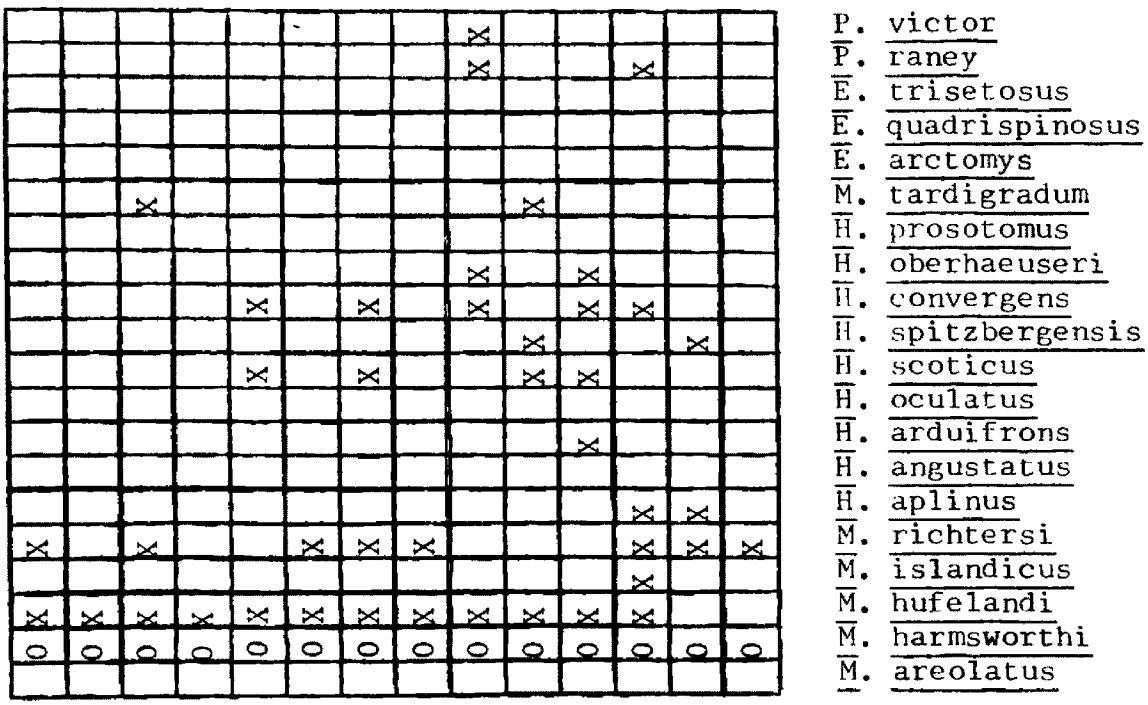


X = Found Together

O = Neutral Square

Sample Number	Habitat for	Substrate	N
	M. islandicus		
19B	Pohlia nutans	soil	1
24 A	Leptodicyum riparium	soil	1
	M. areolatus		
1B	Homalothecium occidentali	rock	1
2C	Claopodium bolanderi	rock	1
	Rnytidiadelphus triquetrus		
3A	Unidentified plant	rock	1
	M. harmsworthi		
2C	Claopodium bolanderi	rock	5
	Rhytidadelphus triquetrus		
1 B	Homalothecium occidentali	rock	2
83B	Homalothecium nevadense	soil	2

Ecological Data for the Genus Macrobiotus



Sample Number	Habitat for M. harmsworthi	Substrate	N
49A	Homalothecium nevadense	soil	1
17A	" "	rock	2
58A	" "	rock	8
18A	Brachytecium albicans	soil	1
20A	" velutinum	soil	5
47D	" lamprochyseum	log	1
54B	Eurynchium pulchellum	log	1
62A	" "	rock	10
23B	Dicranum bonjeani	soil	7
55A	" lauricum	log	1
22B	Hypnum revoltum	rock	14
24A	Leptodictyum riparium	soil	1
36A	Cratoneuron filicinum	rock	16
38 A	Orthotrichum speciosum	soil	1

X = Found Together

O = Neutral Square

Ecological Data for the Genus Macrobiotus

Sample Number	Habitat for	Substrate	N	P. victor	P. raney	E. trisetosus	E. quadrispinosus	E. arctomys	M. tardigradum	H. prosotomus	H. oberhaeuseri	H. convergens	H. spitzbergensis	H. scoticus	H. oculatus	H. arduifrons	H. angustatus	H. aplinus	M. richtersi	M. islandicus	M. hufelandi	M. harmsworthi	M. areolatus
	M. harmsworthi																						
40B	Rhytidiopsis robusta	soil	3													X						O	X
50A	Polytrichum juniperinum	tree	1										X		X							O	X
18B	lichen	soil	1																			O	X
22A	lichen	rock	4					X					X									O	O
47A	lichen	tree	12																			O	
54A	lichen	tree	2															X				O	
60C	lichen	tree	1										X									O	
61C	moss	rock	6																			O	
28C	moss	soil	2															X				O	X
35A	vascular plant	rock	1									X	X						X			O	
50B	lichen	soil	2										X									O	X
	M. hufelandii																						
54B	Eurhynchium pulchellum	log	11												X					X	O	X	
62A	"	rock	1																	X	O	X	
19A	"	soil	1												X						O		

X = Found Together

O = Neutral Square

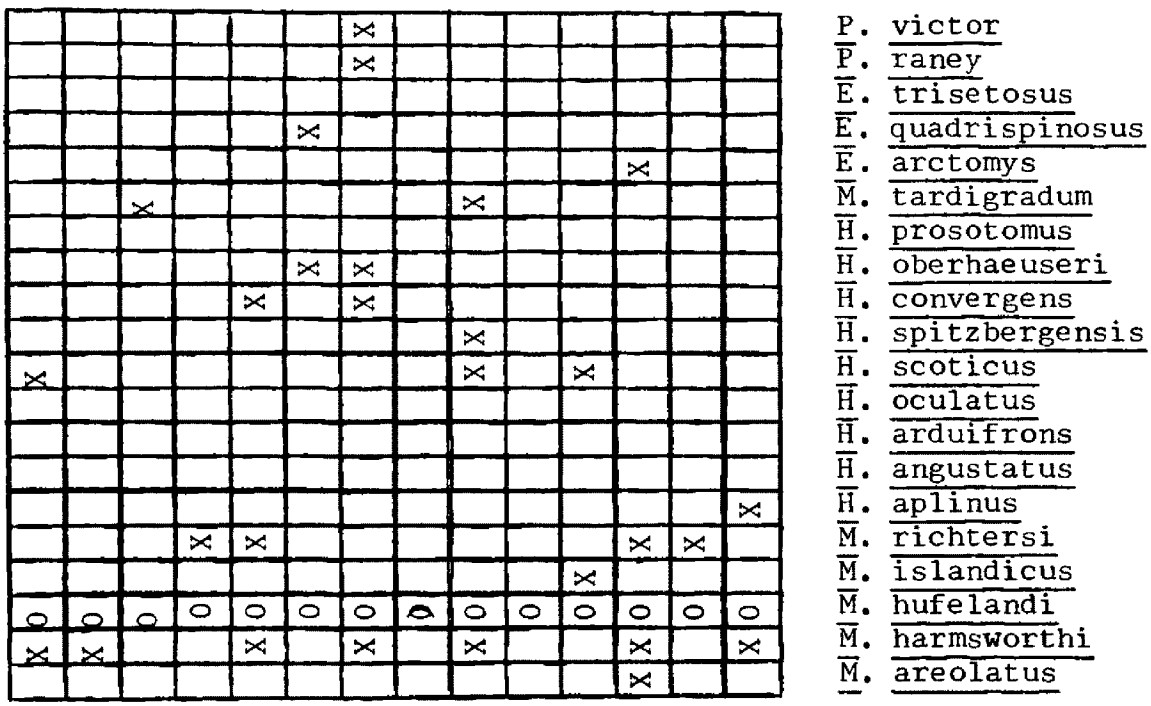
Ecological Data for the Genus Macrobiotus

Sample Number	Habitat for M. hufelandii	Substrate	N	Associated Tardigrada																
				P. victor	P. raney	E. trisetosus	E. quadrispinosus	E. arctomys	M. tardigradum	H. prosotomus	H. oberhaeuseri	H. convergens	H. spitzbergensis	H. scoticus	H. oculatus	H. arduifrons	H. angustatus	H. aplinus	M. richtersi	M. islandicus	M. hufelandi	M. harmsworthi	M. areolatus
79B	Dicrananoweisia crispula	rock	22		X															O			
17A	Homalothecium nevadense	rock	30																O	X			
49A	" "	soil	26																O	X	X		
58A	" "	rock	11					X											O	X	X		
68A	" "	soil	1							X									O		O		
85B	" "	soil	24																O	X	X		
1B	" occidentali	rock	2								X	X		X					O	X	O		
63A	Pleurozium schreberi	soil	17										X						O		O		
60B	Sphagnum sp.	soil	1																O		O		
61B	Fissidens cristatus	----	-																O		O		
22B	Hypnum revolutum	rock	4																O	X	O		
2A	Timmia austriaca	rock	3									X	X						O		O		
4C	Pseudoleskea patens	----	7														X		O		O		
61A	Drepanocladus aduncus	aqua	1									X							O		O		

X = Found Together

O = Neutral Square

Ecological Data for the Genus Macrobiotus



Sample Number	Habitat for M. hufelandii	Substrate	N
20A	Brachythecium velutinum	soil	5
18A	" albicans	soil	2
57A	" "	soil	21
84A	" "	soil	5
47D	" "	log	2
11B	Dicranum bonjeani	soil	10
23B	" "	soil	2
60D	" fuscnscens	soil	28
55A	" tauricum	log	9
60D	Pohlia nutans	----	--
19B	" "	soil	11
2C	Rhytidiadelphus triquetrus	rock	27
28B	" "	soil	27
40B	" robusta	soil	23

X = Found Together

O = Neutral Square

Ecological Data for the Genus *Macrobiotus*

Sample Number	Habitat for *M. hufelandii*	Substrate	N
50A	*Polytrichum juniperinum*	tree	1
63A	" "	log	22
61B	*Bryum pseudotriquetrum*	rock	1
24A	*Leptodictyum riparium*	---	2
1D	moss	rock	1
61C	moss	soil	58
4D	lichen	tree	6
12B	lichen	rock	3
18B	lichen	soil	1
22A	lichen	rock	1
50B	lichen	soil	22
3A	vascular plant	rock	4
30A	fungi	soil	4

Associated Tardigrada

	50A	63A	61B	24A	1D	61C	4D	12B	18B	22A	50B	3A	30A
P. victor				X							X		
P. raney													
E. trisetosus	X												
E. quadrispinosus	X			X						X	X	X	
E. arctomys											X		
M. tardigradum													
H. prosotomus								X					
H. oberhaeuseri													
H. convergens										X	X	X	
H. spitzbergensis				X								X	
H. scoticus													
H. oculatus													
H. arduifrons													
H. angustatus													
H. aplinus				X		X							
M. richtersi				X									
M. islandicus				X									
M. hufelandi	0	0	0	0	0	0	0	0	0	0	0	0	0
M. harmsworthi	X						X		X	X	X		
M. areolatus												X	

X = Found Together

O = Neutral Square

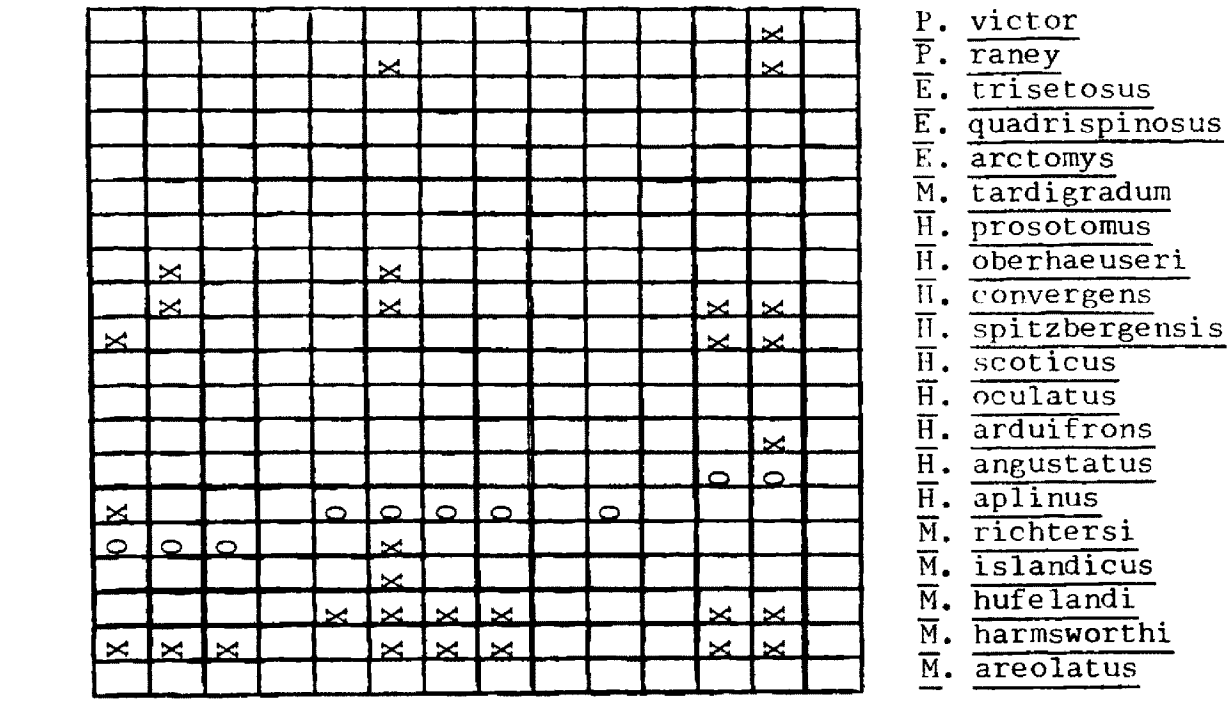
Ecological Data for the Genus *Macrobiotus*

Sample Number	84A	47D	54B	62A	2C	85B	49A	58A	1B	28B	38A	24A	63B	63A
Habitat for *M. richtersi*	*Brachythecium albicans*	" *lamprochryseum*	*Eurhynchium pulehellum*	" "	*Claopodium bolanderi*	*Rhytidiadephus triquetrus*	*Homalothecium nevadense*	" "	" *occidentali*	*Rhytidiadephus triquetrus*	*Orthotrichum speciosum*	*Leptiodictyum riparium*	*Polytrichum juniperinum*	*Pleurozium sehreberi*
Substrate	soil	log	log	rock	rock	soil	soil	rock	rock	----	soil	soil	log	soil
N	25	1	2	9	4	1	2	4	1	1	2	2	1	13
Associated Tardigrada														
P. victor														
P. raney												X		
E. trisetosus														
E. quadrispinosus														
E. arctomys					X									
M. tardigradum								X						
H. prosotomus														
H. oberhaeuseri									X					
H. convergens		X	X						X			X		X
H. spitzbergensis														
H. scoticus			X											
H. oculatus									X					
H. arduifrons														
H. angustatus														
H. aplinus												X		
M. richtersi	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M. islandicus												X		
M. hufelandi	X	X	X	X	X	X	X	X	X	X		X	X	X
M. harmsworthi		X	X	X	X	X	X	X	X		X	X		
M. areolatus					X				X					

X = Found Together

0 = Neutral Square

Ecological Data for the Genera *Macrobiotus* and *Hypsibius*



Sample Number	Habitat for *M. richtersi*	Substrate	N
36A	*Crataneurons filicium*	rock	20
35A	vascular plant	rock	2
54A	lichen	tree	1
	Hypsibius alpinus		
4C	*Pseudoleskea patens*	----	1
24A	*Leptodictym riparium*	soil	1
40B	*Rhytidiopsis robusta*	soil	1
61C	moss	soil	6
	Hypsibius angustatus		
20B	*Pogonatum alpinum*	soil	1
	Hypsibius arduifrons		
22B	*Hypnum revoltum*	rock	6
23B	*Dicranum bonjeani*	soil	3

X = Found Together

O = Neutral Square

Ecological Data for the Genus *Hypsibius*

Sample Number	Habitat for *H. oculatus*	Substrate	N	Associated Tardigrada																		
				P. victor	*P. raney*	*E. trisetosus*	*E. quadrispinosus*	*E. arctomys*	*M. tardigradum*	*H. prosotomus*	*H. oberhaeuseri*	*H. convergens*	*H. spitzbergensis*	*H. scoticus*	*H. oculatus*	*H. arduifrons*	*H. angustatus*	*H. aplinus*	*M. richtersi*	*M. islandicus*	*M. hufelandi*	*M. harmsworthi*	*M. areolatus*
1B	*Homalothecium occidentali*	rock	1	X	X									0		X	X						
23B	*Dicranum fuscescens*	soil	1			X								0									
28C	Moss	rock	1	X						X				0									
36A	*Cratoneuron filicunum*	rock	1	X										0			X	X					
	H. scoticus																						
20A	*Brachytecium velutinum*	soil	1	X	X									0									
50A	*Polytrichum juniperinum*	tree	1	X	X								X	0									
55A	*Dicranum tauricum*	log	2		X									0	X								
60B	*Sphagnum sp.*	bog	1											0									
54B	*Eurhynchium pulchellum*	log	1	X	X								X	0					X				
	H. spitzbergensis																						
55A	*Dicranum tauricum*	log	1		X									X	0								
19A	*Eurhynchium pulchellum*	soil	1		X	X						X		0									
3A	vascular plant	rock	1	X		X									0	X							

X = Found Together

0 = Neutral Square

Ecological Data for the Genus *Hypsibius*

Associated Tardigrada

	1B	68A	22B	23B	24A	47D	50A	54B	61A	63A	22A	60C	3A	35A
P. victor				X										
P. raney				X	X									
E. trisetosus														
E. quadrispinosus														
E. arctomys														
M. tardigradum														
H. prosotomus														
H. oberhaeuseri	X		X	X										X
H. convergens	0	0	0	0	0	0	0	0	0	0	0	X	0	0
H. spitzbergensis													X	
H. scoticus							X							
H. oculatus	X													
H. arduifrons			X	X										
H. angustatus														
H. aplinus					X									
M. richtersi	X				X	X		X		X				X
M. islandicus					X									
M. hufelandi	X	X	X	X	X	X	X	X	X	X	X		X	
M. harmsworthi	X		X	X	X	X	X	X			X	X		X
M. areolatus	X												X	

Sample Number	Habitat for *H. convergens*	Substrate	N
1B	*Homalothecium occidentali*	rock	1
68A	" *nevadense*	soil	1
22B	*Hypnum revolutum*	rock	15
23B	*Dicranum bonjeani*	soil	9
24A	*Leptodictyum riparium*	soil	1
47D	*Brachythecium lamprochryseum*	soil	1
50A	*Polytrichum juniperinum*	tree	3
54B	*Eurhynchium pulchellum*	soil	1
61A	*Drepanocladus aduncus*	aqua	1
63A	*Pleurozium sehreberi*	soil	1
22A	lichen	rock	1
60C	lichen	tree	1
3A	plant	rock	8
35A	plant	---	3

X = Found Together

0 = Neutral Square

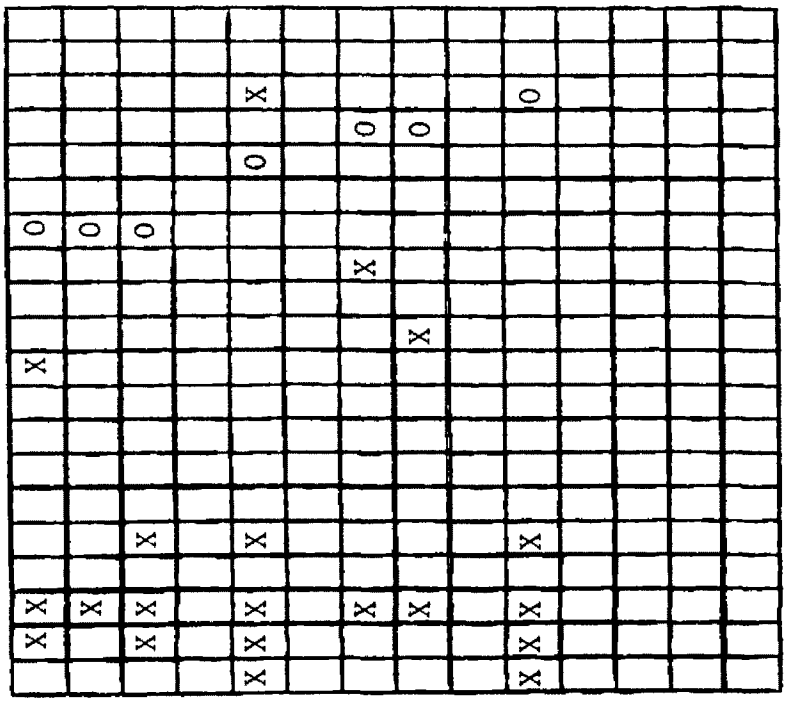
Ecological Data for the Genus *Hypsibius*

Sample Number	Habitat for *H. oberhaeuseri*	Substrate	N	Associated Tardigrada																					
				P. victor	*P. raney*	*E. trisetosus*	*E. quadrispinosus*	*E. arctomys*	*M. tardigradum*	*H. prosotomus*	*H. oberhaeuseri*	*H. convergens*	*H. spitzbergensis*	*H. scoticus*	*H. oculatus*	*H. arduifrons*	*H. angustatus*	*H. aplinus*	*M. richtersi*	*M. islandicus*	*M. hufelandi*	*M. harmsworthi*	*M. areolatus*
1B	*Homalothecium occidentali*	rock	1								X	O			X				X	X		X			X
11B	*Dicranum bonjeani*	soil	2				X					O								X					
22B	*Hypnum revoltum*	rock	1								X	O								X	X				
23B	*Dicranum bonjeani*	soil	4								X	O				X				X	X				
79B	*Dicranowisia crispula*	rock	1									O								X	X				
50A	*Polytrichum juniperinum*	tree	2									O			X					X	X				
4A	Aquatic mosses	aqua	2									O													
12B	lichen	rock	16									O								X					
19C	lichen	tree	3									O													
22A	lichen	rock	1									O								X	X				
35A	vascular plant	----	2								X	O							X						
	H. prosostomus																								
28C	moss	rock	1							O												X			

X = Found Together

O = Neutral Square

Ecological Data for the Genera Milnesium and Echiniscus



Associated Tardigrada

P. victor
P. raney
E. trisetosus
E. quadrispinosus
E. arctomys
M. tardigradum
H. prosotomus
H. oberhaeuseri
H. convergens
H. spitzbergensis
H. scoticus
H. oculatus
H. arduifrons
H. angustatus
H. aplinus
M. richtersi
M. islandicus
M. hufelandi
M. harmsworthi
M. areolatus

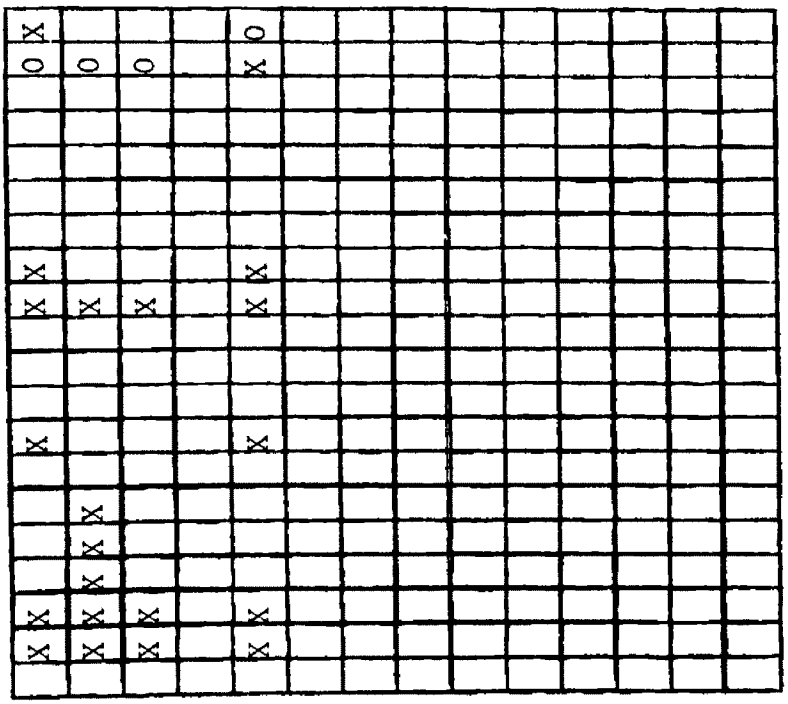
Sample Number	Habitat for	Substrate	N
	M. tardigradium		
55A	Dicranum tauricum	log	2
57A	Brachythecium albicans	soil	1
58A	Homalothecium nevadense	rock	2
	Echiniscus arctomys		
2C	Rhytidiadezphus triquetrus	rock	3
	Echiniscus quadrispinosus		
11B	Dicranum bonjeani	soil	1
19A	Eurhynchium pulchellum	soil	1
	Echiniscus trisetosus		
2C	Rhytidiadezphus triquetrus	rock	1

X = Found Together

O = Neutral Square

Ecological Data for the Genus Pseudechiniscus

Associated Tardigrada



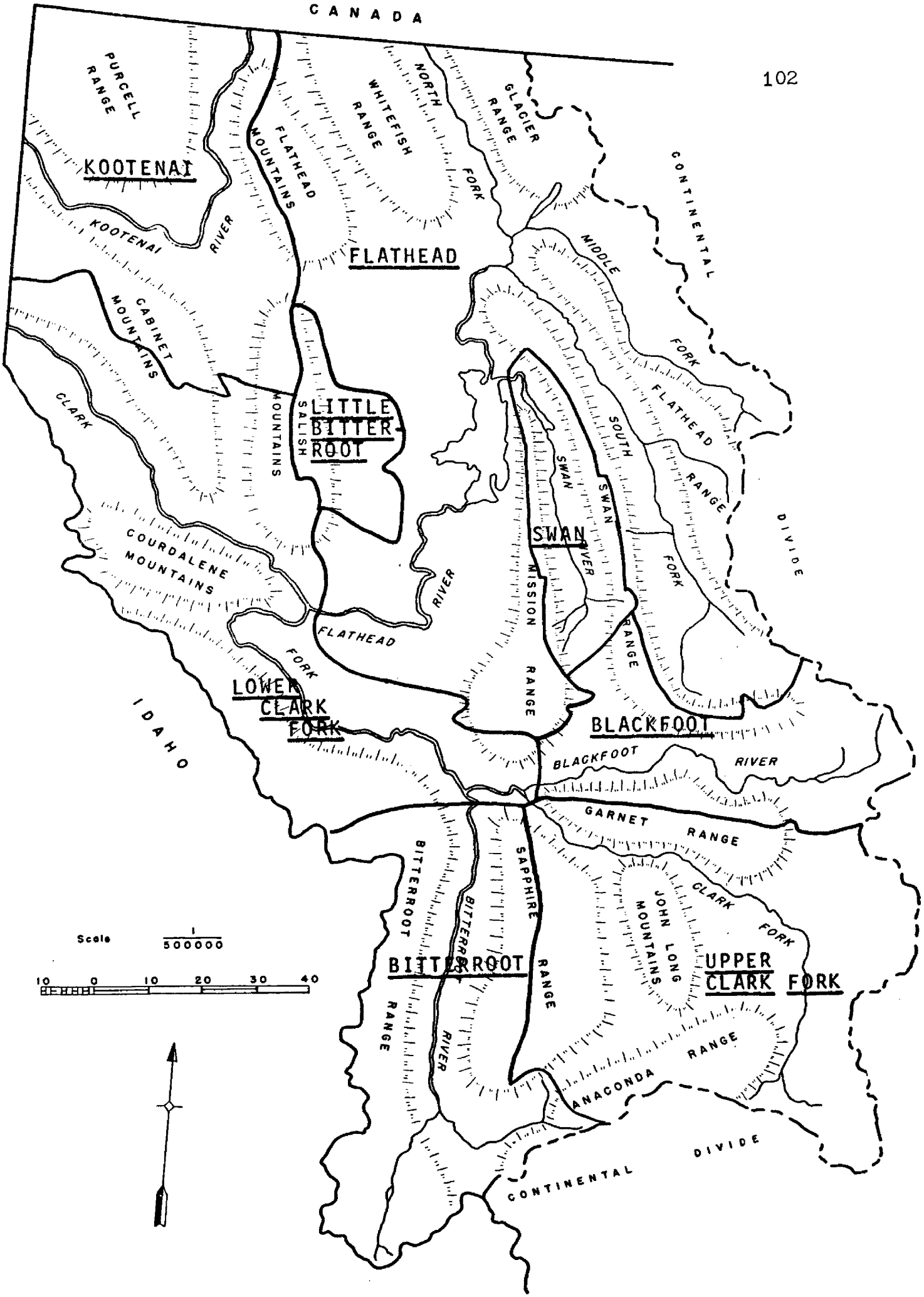
P. victor
P. raney
E. trisetosus
E. quadrispinosus
E. arctomys
M. tardigradum
H. prosotomus
H. oberhaeuseri
H. convergens
H. spitzbergensis
H. scoticus
H. oculatus
H. arduifrons
H. angustatus
H. aplinus
M. richtersi
M. islandicus
M. hufelandi
M. harmsworthi
M. areolatus

X = Found Together

O = Neutral Square

Sample Number	Habitat for	Substrate	N
	P. raneyi		
23B	*Dicranum bonjeani*	soil	1
	Leptodictyum riparium		
24A		soil	1
50B	lichen	soil	3
	P. victor		
23B	*Dicranum bonjeani*	soil	4

Map 1. Major Watersheds of Western Montana

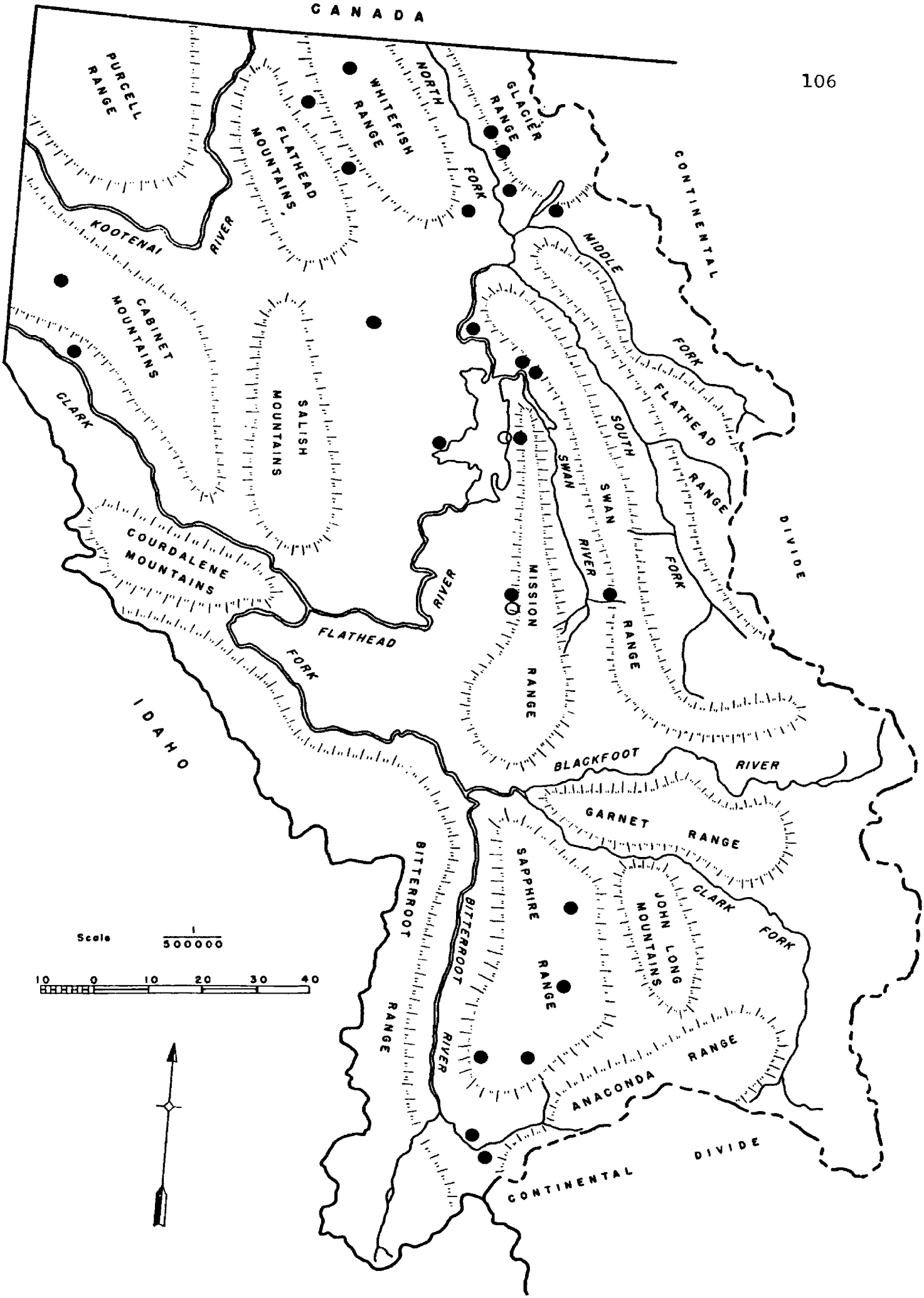


Map 2. Counties of Western Montana

Map 3. Distribution of *Macrobiotus areolatus* and *Macrobiotus harmsworthi* in Western Montana

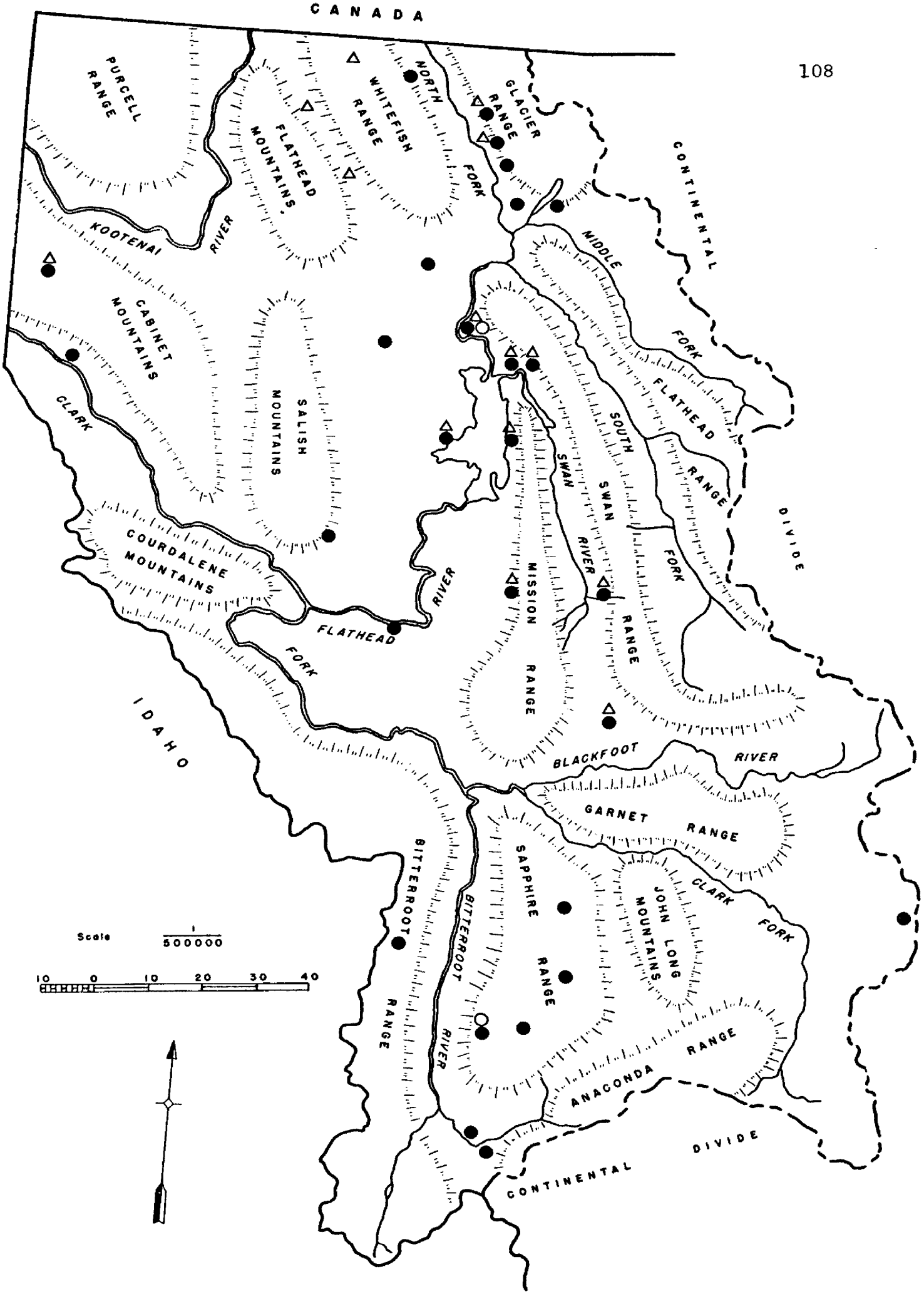
Macrobiotus areolatus ○

Macrobiotus harmsworthi ●



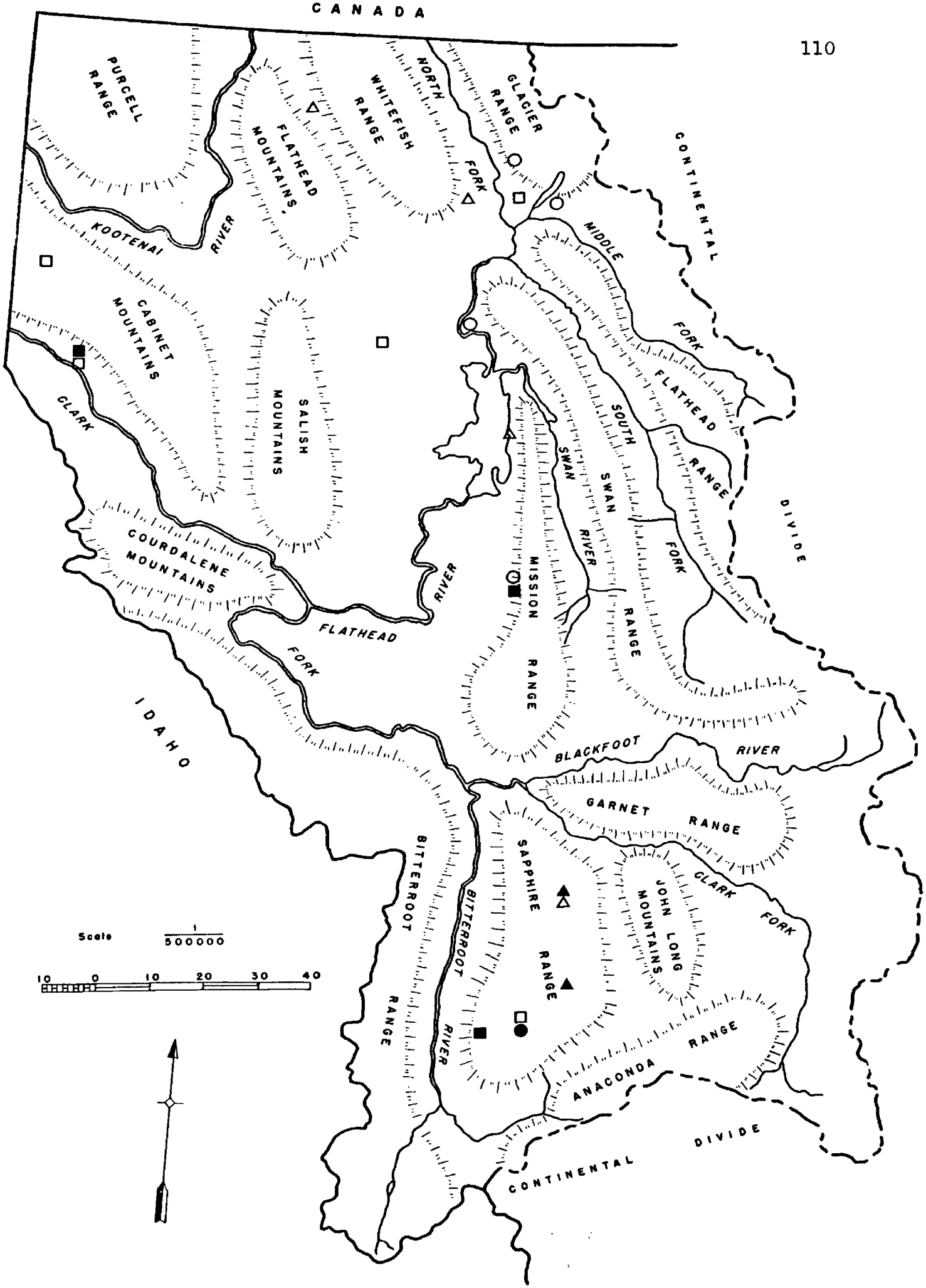
Map 4. Distribution of Macrobiotus hufelandii, Macrobiotus islandicus, and Macrobiotus richtersi in Western Montana

Macrobiotus hufelandii ●
Macrobiotus islandicus ○
Macrobiotus richtersi △



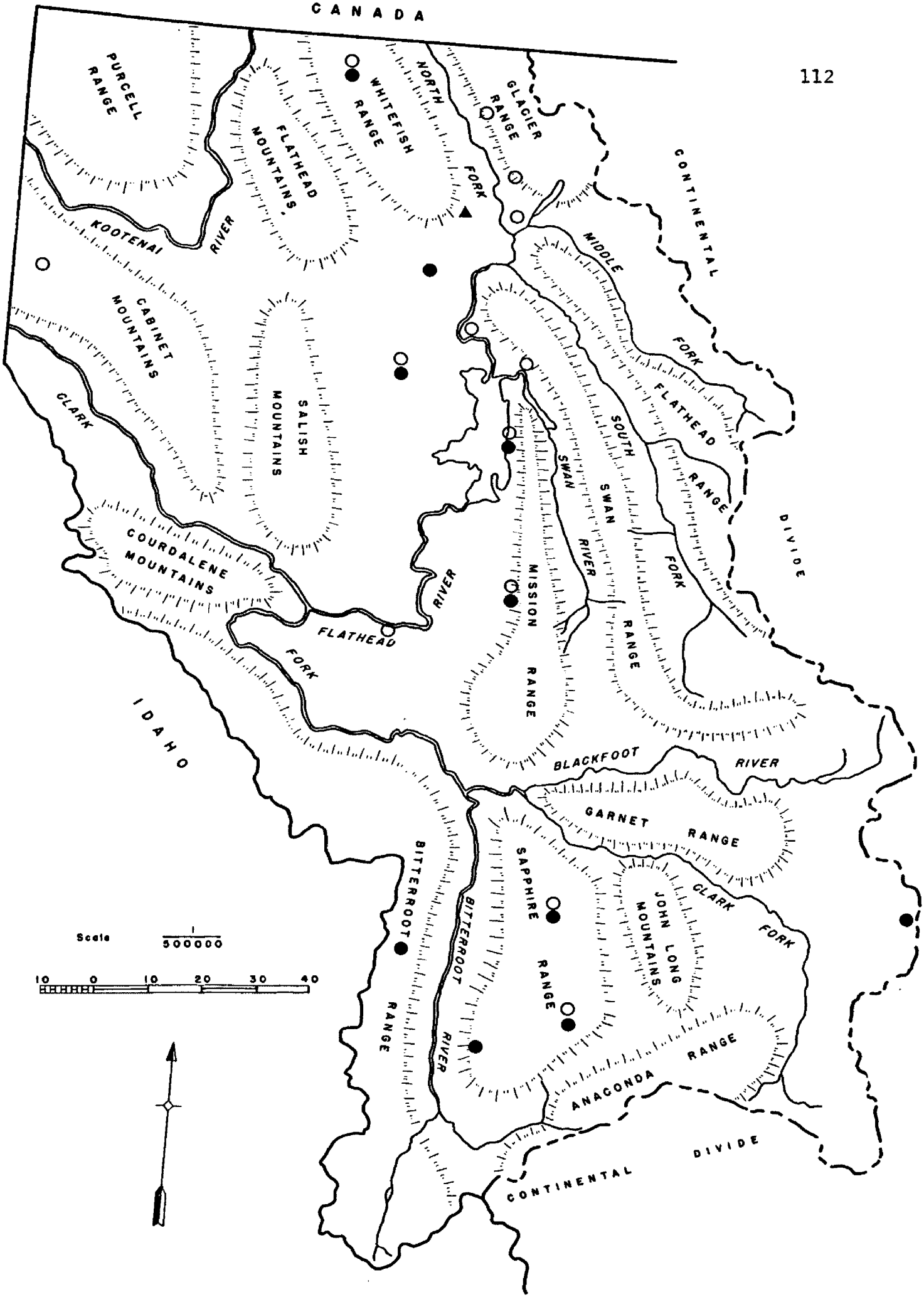
Map 5. Distribution of Hypsibius alpinus, Hypsibius angustatus, Hypsibius arduifrons, Hypsibius oculatus, Hypsibius scoticus, and Hypsibius spitzbergensis in Western Montana

Hypsibius alpinus ○
Hypsibius angustatus ●
Hypsibius arduifrons ▲
Hypsibius oculatus △
Hypsibius scoticus □
Hypsibius spitzbergensis ■



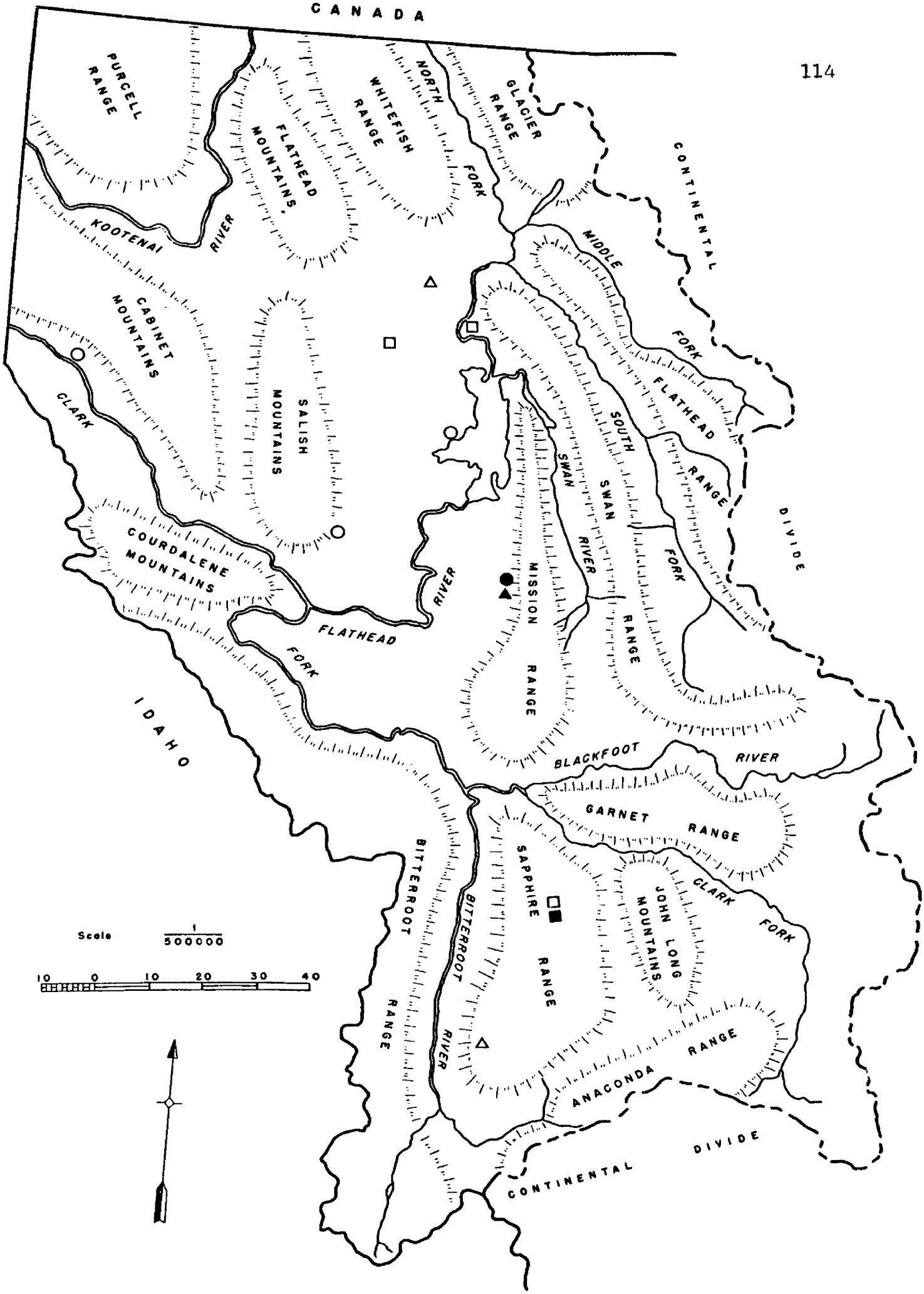
Map 6. Distribution of Hypsibius convergens, Hypsibius oberhaeuseri, and Hypsibius prosostomus in Western Montana

Hypsibius convergens ○
Hypsibius oberhaeuseri ●
Hypsibius prosostomus ▲



Map 7. Distribution of Milnesium tardigradum, Echiniscus arctomys, Echiniscus quadrispinosus, Echiniscus trisetosus, Pseudechiniscus raneyi, and Pseudechiniscus victor in Western Montana

Milnesium tardigradum	○
Echiniscus arctomys	●
Echiniscus quadrispinosus	△
Echiniscus trisetosus	▲
Pseudechiniscus raneyi	□
Pseudechiniscus victor	■

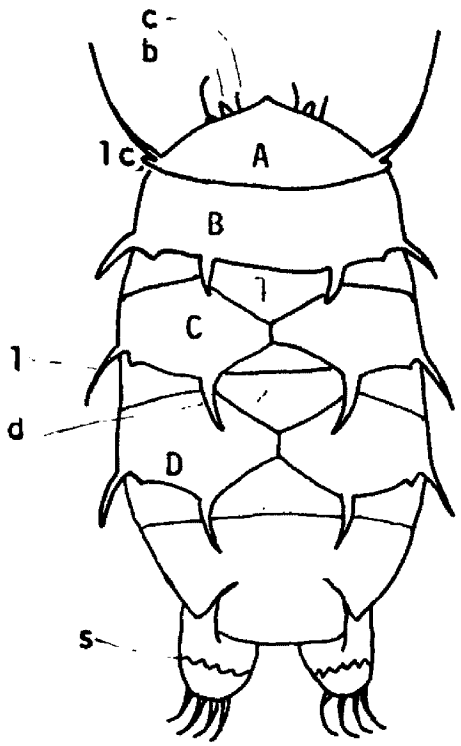


PLATES

Plate 1. Dorsal plate structure of *Echiniscus* and *Pseudechiniscus*

Fig. A *Echiniscus*

Fig. B *Pseudechiniscus*



A-E Dorsal plates
1-3 Intersegmental plates
c Buccal cirri (internal & external)
b Buccal papilla
1 Lateral spine
d Dorsal spine
1c Lateral cirri A.
s Collar on leg IV

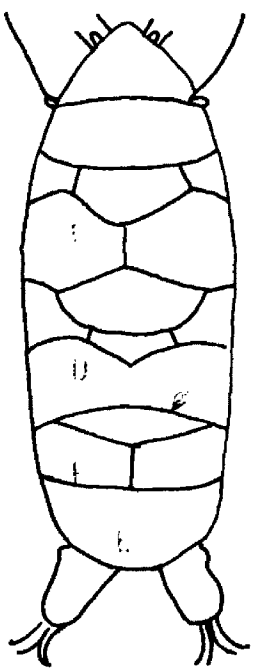
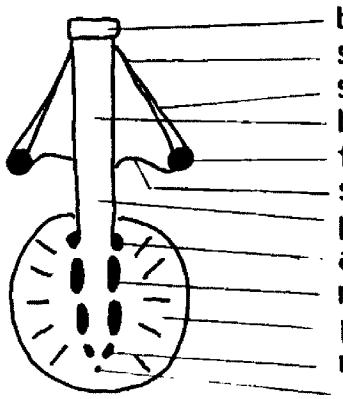


Plate 2. General structure of mouth parts and claws of *Milnesum*, *Microbiotus*, and *Hypsibius*.

Fig. A. Mouth parts
Fig. B. Claw structure of *Milnesium*
Fig. C. Claw structure of *Macrobiotus* (*M. hufelandii* - type)
Fig. D. Claw structure of *Hypsibius*



b Buccal ring
ss Stylet sheath
s Stylet
bt Buccal tube
f furcae
ssu Stylet support
p Pharyngeal tube
a Apophysis
ma Macroplacoid
ph Pharynx
mi Microplacoid
se Septulum

Fig A.

Fig. B.

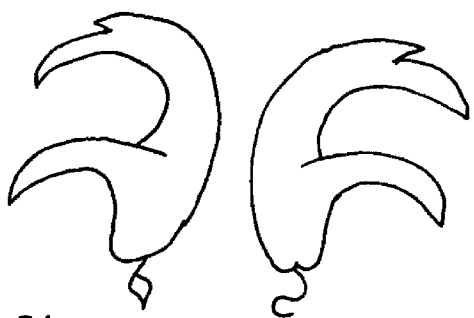


Fig. .

Fig. D.

Plate 3. Mouth parts of *Macrobiotus*

Fig. A *M. areolatus*
Fig. B *M. harmsworthi*
Fig. C *M. hufelandii*
Fig. D *M. richtersi*
Fig. E *M. islandicus*

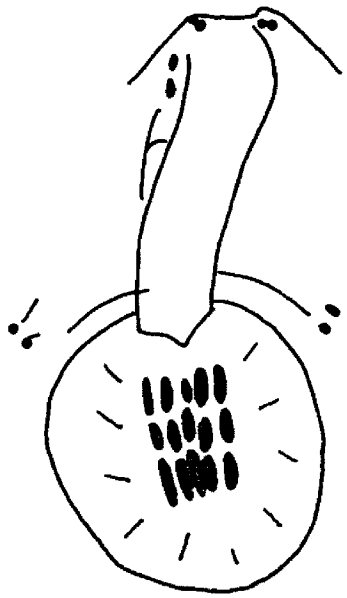


Fig. A.

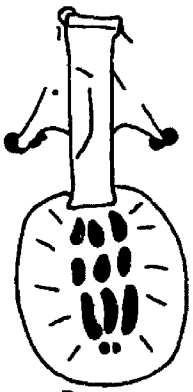


Fig. B.

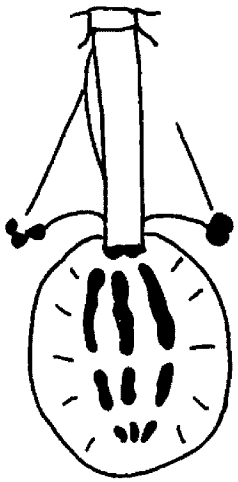


Fig. C.

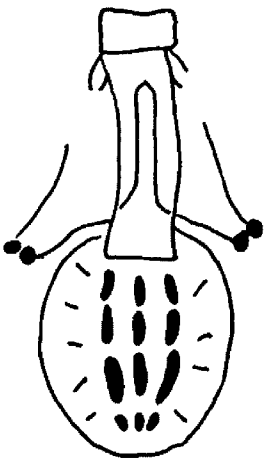


Fig. D.

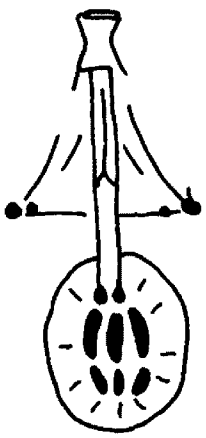


Fig. E.

Plate 4. Mouth parts of *Hypsibius*

Fig. A *H. alpinus*
Fig. B *H. angustatus*
Fig. C *H. oculatus*
Fig. D *H. scoticus*
Fig. E *H. spitzbergensis*
Fig. F *H. prosostomus*

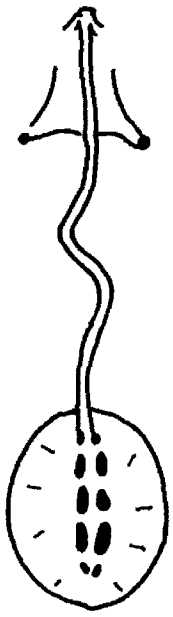


Fig. A.

Fig. B.

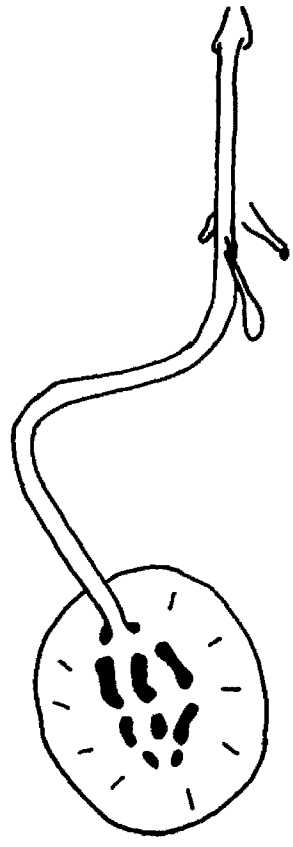


Fig. C.

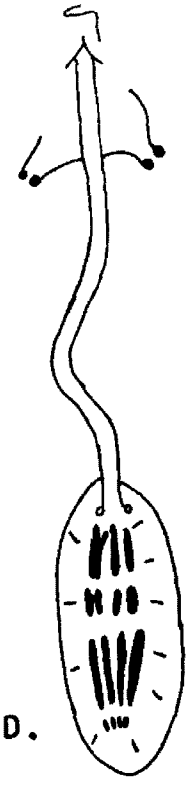


Fig. D.

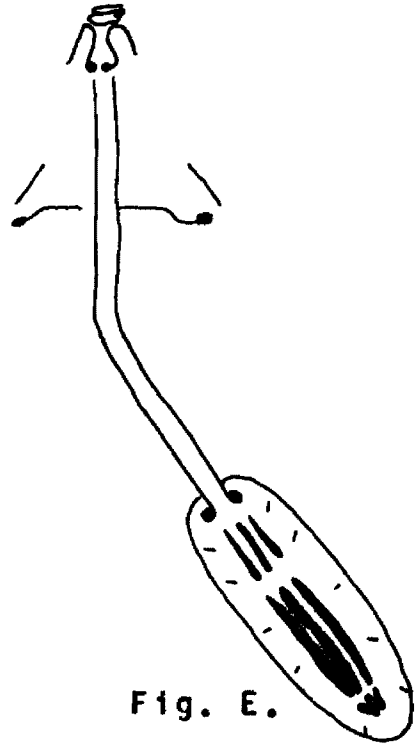


Fig. E.

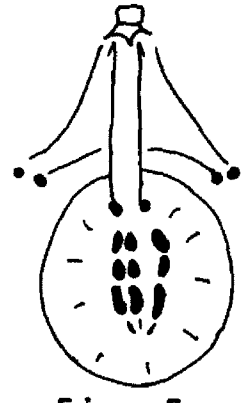


Fig. F.

Plate 5. Mouth parts of *Hypsibius* and *Milnesium*

Fig. A *H. convergens*
Fig. B *H. oberhaeuseri*
Fig. C *M. tardigradum*
Fig. D-I *H. arduifrons*

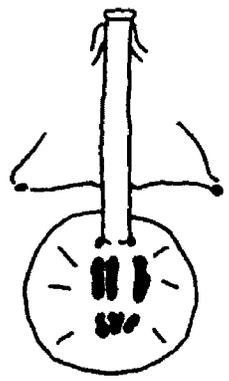


Fig. A.

Fig. B.

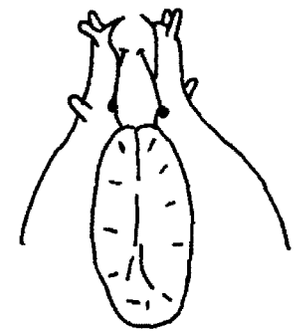


Fig. C.

Fig. D.

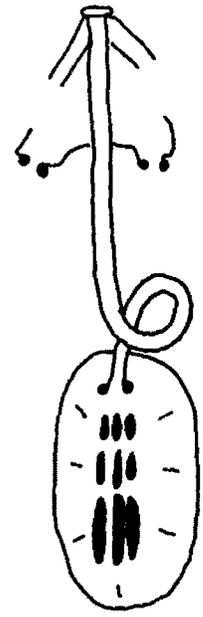


Fig. E.

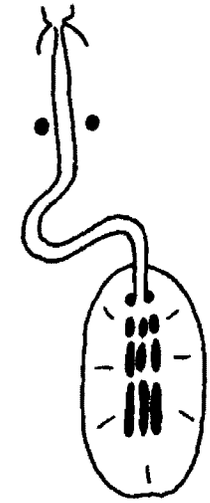


Fig. F.

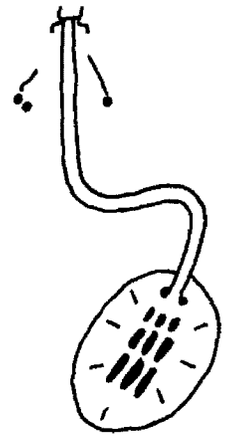


Fig. G.

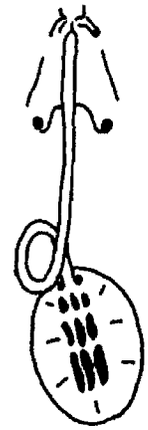


Fig. H.

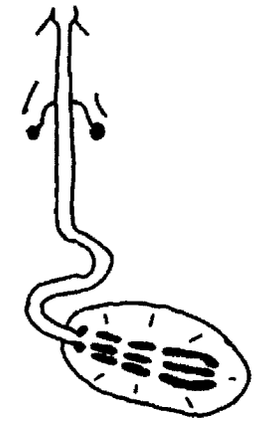


Fig. I.

GLOSSARY

Accessory sac	Bulbous structure attached to pharyngeal tube, function unknown.
Apodeme	Structure supporting buccal tube in the genus Macrobiotus.
Apophysis	Expanded base of pharyngeal tube, inside pharynx.
Buccal ring	Mouth, area around mouth.
Buccal tube	Mouth tube, from buccal ring to stylet supports.
Cirri	Spine-like projections not arising from a plate.
Dorsal plate	Hard, jointed plate-like structures on the dorsal surface of some tardigrades.
Furcae	Joint between stylet and stylet.
Intersegmental plate	Smaller plate between dorsal plates.
Macroplacoid	Sclerotized structure in pharynx for grinding food, up to three sets may be present.
Microplacoid	Sclerotized structure in pharynx, small, located posteriad of macroplacoids, may be absent.
Papillae	Rounded, fleshy projection.
Pharyngeal tube	Tube between buccal tube and pharynx.
Pharynx	Muscular, expandable, structure at end of pharyngeal tube, containing placoids, and used for feeding.

Septulum	Sclerotized structure in pharynx, posteriad to microplacoid.
Spine	Long, thin extension of a plate.
Stylet	Needle-like structure flanking buccal tube used to pierce food items.
Stylet sheath	Tube into which stylet is withdrawn.
Stylet support	Muscle bands connecting buccal tube and stylet, joining at furcae.

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